The taxonomy of the western European grasshoppers of the genus *Euchorthippus*, with special reference to their songs (Orthoptera: Acrididae)

D. R. Ragge & W. J. Reynolds
Department of Entomology, British Museum (Natural History), Cromwell Road, London
SW7 5BD

Contents

Synopsis 103
Introduction 103
Acknowledgements 104
Material 105
Methods 105
  Morphology 105
  Song 106
  Presentation and evaluation of the data 110
Characters studied 111
  Morphology 111
  Colour pattern 117
  Cytology 117
  Song 117
Euchorthippus Tarbinskii 121
  Key to the western European and North African species
    and subspecies of *Euchorthippus* 122
  Descriptions of the species 125
General discussion 139
References 141
Index 151

Synopsis

The taxonomy of the western European species and subspecies of the Gomphocerine genus *Euchorthippus* is re-examined on the basis of both morphological and song characters, making full use of such visual aids as bar-charts and scatter diagrams. It is shown that the past emphasis on the male subgenital plate as a diagnostic character has resulted in the frequent misidentification of the three main species, *declivus*, *pulvinatus* and *chopardi*. This has been particularly true in Spain, where *pulvinatus* and *chopardi* have often been misidentified as *declivus* and *pulvinatus*, respectively. It is also shown that the Jersey form *elegantulus*, previously synonymized with *declivus*, is actually a form of *pulvinatus*, and that a further population of it occurs in southern Brittany. Analyses of the songs of these species, previously thought to be of little taxonomic value, have provided strong support for these conclusions. The study embraces four further taxa known only from the western Mediterranean islands or North Africa, and the song of the Balearic species *angustulus* is fully described and analysed for the first time. Keys are given for the identification of all these species and subspecies, and their evolution and rather anomalous present distribution are briefly discussed.

Introduction

Euchorthippus belongs to the Gomphocerinae, a group that includes most of the common European grasshoppers of open grassland. They are well known for their characteristic – and taxonomically useful – songs, and are frequently used in ecological and cytological studies. The subfamily includes about 150 European species, of which over 20 are pests in parts of their range, seven of them being regarded as major ones (Tsyplenkov, 1970).

Bull. Br. Mus. nat. Hist. (Ent.) **49** (2): 103–151 Issued 26 July 1984

Euchorthippus is a widespread Palaearctic genus, including 14 species living in habitats ranging from moist grassland to steppe and barren hillside. Five species occur in western Europe and one of these, *E. pulvinatus*, becomes a pest when it occurs in sufficiently dense populations, causing damage to pastureland, hayfields, cereal grasses, alfalfa and other cultivated plants in western and, especially, eastern Europe (Bei-Bienko & Mishchenko, 1951; Tsyplenkov, 1970). This species sometimes reaches densities of over 10/m^2 in the *Stipa*-steppe areas of the Ukraine and northern Kazakhstan, where it is by far the most numerous grasshopper (Chetyrkina, 1954; Bei-Bienko, 1961).

Euchorthippus is quite easy to recognize as a genus, but its species are much more difficult to identify and have frequently been confused with one another. *E. declivus, E. pulvinatus* and *E. chopardi* form a group of closely similar species that are very difficult to separate using the keys at present available. Among more recent studies of this group, those of Mařan (1957), Descamps (1968), Litvinova (1972) and Defaut (1982) have much improved our knowledge of their taxonomy, ecology and geographical variation. The songs of these species have been described briefly by Descamps (1968), Luquet (1978) and Schmidt & Schach (1978), but these authors attached little or no taxonomic importance to the differences between them. The main aim of our study has been to refine further the best methods for distinguishing morphologically between these species and to demonstrate the taxonomic importance of their songs.

Although we have concentrated our study on this group of three species, for each of which we have been able to study the song, we have also included morphological information on all the other species occurring in western Europe and North Africa and, in the case of *E. angustulus*, have been able to give full information on the song for the first time. The geographical area covered by our study consists of southern Europe and the Mediterranean Region from Italy westwards, including North Africa.

Morphological recognition of the species of *Euchorthippus* depends mainly on differences in size and proportion, and we have chosen to present this information in the form of visual aids such as bar-charts and scatter diagrams so that the most important differences can be seen at a glance and a specimen can be identified quickly by entering its key measurements on the appropriate diagram. Similar visual aids have been used to illustrate the significance of the differences in song.

E. pulvinatus pulvinatus, which does not occur in western Europe, is excluded from our study, and where the specific name '*pulvinatus*' is used in our text it refers only to the western subspecies *E. p. gallicus* and *E. p. elegantulus* unless otherwise indicated.

Acknowledgements

We are much indebted to the following, who have kindly lent us type-specimens or other material from their respective institutions:

Drs A. Čejchan, G. Demoulin, M. Donskoff, M. J. González, K. K. Günther, L. Herrera, G. Kruseman, V. Llorente and E. Tremblay.

We are also grateful to Dr A. Nadig for lending us the holotype of *E. sardous* from his private collection in Chur, Switzerland; to Dr B. Defaut, who lent us specimens of *Euchorthippus* from Brittany and Teruel province in Spain; and to Mr D. W. Baldock, who gave us, among other specimens, a female *Euchorthippus* from Guérande in southern Brittany and thus alerted us to the occurrence there of the interesting small form of *E. pulvinatus* (see p. 131). We thank Mr J. F. Burton for very kindly making available to us a tape recording of the song of a male *Euchorthippus* from Jersey.

Our thanks are due to Messrs W. G. Tremewan and B. C. Townsend, who collected live males for us from Spain and Jersey, respectively, and thus enabled us to make studio song recordings from them; to Mr E. C. M. Haes, who collected specimens for us from France; to Mr W. B. Lee, who helped us to obtain data from specimens and song oscillograms; to Dr M. Hills of the British Museum (Natural History) Biometrics and Computing Section, who advised us on statistical methods; and to Dr F. Willemse for information on the distribution of *Euchorthippus* in Greece.

Finally we should like to thank Mr P. H. Ward for his skilful preparation of the drawings shown in Figs 25–30.

Material

Our study is based almost entirely on material in the British Museum (Natural History), amounting to about 1500 western European specimens of *Euchorthippus*. Many of these specimens were collected by us during recent visits to France and Spain.

The song analyses were based on tape recordings made by us in the field in France and Spain, and in the BMNH Acoustic Laboratory from males brought back from Jersey, France, Spain and Majorca; we were also able to make use of a tape recording kindly made available to us by Mr J. F. Burton.

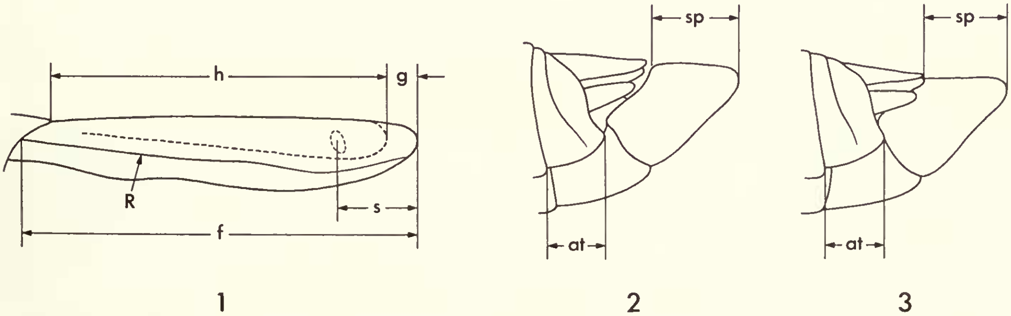
We have used the following abbreviations for depositories of type-specimens.

BMNH	British Museum (Natural History), London
IEA	Istituto di Entomologia Agraria, Portici
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin
NM	Národní Muzeum, Prague

Methods

Morphology

The morphological measurements were made using a Wild M5 microscope with a graduated eyepiece. The lengths of the head and pronotum were measured along the mid-line. The length of the fore wing was measured from the tip to the point where the fused subcostal, radial and medial veins of the flexed wing pass under the edge of the pronotum (Fig. 1, f). The length of the hind wing was measured (also when flexed) from the tip of the wing to the median posterior point of the pronotum rather than to the base of the hind wing, since this is hidden under the fore wing when the wings are flexed (Fig. 1, h). The distance from the stigma to the tip of the fore wing was measured from the centre of the stigma, which is more easily determined than its edge (Fig. 1, s). The distance by which the fore wing projected beyond the hind wing was determined by illuminating the flexed wings from below and measuring the distance between the tips of the fore and hind wings (Fig. 1, g). When the hind wing projected beyond the fore wing, the measurement was regarded as negative. The length of the hind femur was measured from the most proximal to the most distal points.



Figs 1–3 Diagrams of (1) the flexed wings and (2, 3) male terminal abdominal segments in species of *Euchorthippus*, showing the method of measuring the length of the fore wing (f), length of the hind wing (h), distance from the stigma to the tip of the fore wing (s), projection of the fore wing beyond the hind wing (g), length of the male subgenital plate (sp) and length of male abdominal tergites 9+10 (at). R = radius. (See also the explanation in the text.)

When counting the stridulatory pegs it was sometimes necessary to relax the leg and to move it away from the body so that the stridulatory file was visible. The pegs were viewed from above, in profile, and were counted as they moved past a line on the microscope eyepiece scale. Following Perdeck (1957), bristles were included in the row and, in determining the ends of the file, a peg or bristle was excluded if its distance from the preceding peg was twice, or more than twice, the distance between the two preceding ones. The length of the stridulatory file was measured from one terminal peg or bristle (determined as above) to the other.

The lengths of the male subgenital plate and abdominal tergites 9+10 were measured following the method used by Descamps (1968) (Fig. 2) except that, when the proximal dorsal edge of the subgenital plate was hidden, the length of only the visible part of the plate was measured (Fig. 3).

As we had at our disposal well over 500 specimens of each of the two common species *declivus* and *pulvinatus*, we measured only a sample of them, following the principle that all the localities from which the specimens came should be represented by at least one measured specimen. We restricted our measurements of *albolineatus* to 10 specimens of each sex, since this North African species was outside the main scope of our study.

Song

All the field recordings of the songs used in this study were made while the insects were in full sunshine using a Uher 4000, 4200 or 4200IC tape recorder and an AKG D202 microphone. Most of the studio recordings were made in the BMNH Acoustic Laboratory using a Kudelski Nagra IV tape recorder and Sennheiser MKH405 microphone. Recording 163 was made from a captive insect by Mr J. F. Burton using a Nagra III tape recorder. The only other recordings not made in the field (179/6, 179/9, 180/1, 180/2) were recorded at the Station Biologique d'Arcachon, Gironde, France, using a Uher 4000 tape recorder and AKG D202 microphone. For all the studio recordings a bench lamp was used to provide light and radiant heat. Further data are given in Tables 1 and 2.

The acoustic terms we have used are defined as follows.

Calling song. The song produced by an isolated male.

Courtship song. The special song produced by a male when close to a female.

Syllable. The sound produced by one complete up and down movement of the hind legs (Fig. 4).

Echeme. A first-order assemblage of syllables (Fig. 4). (Term introduced by Broughton, 1976.)

All the song measurements were taken from oscillograms made with a Mingograf 34T ink-jet recorder. Echeme duration was measured from the end of the first clearly visible syllable to the end of the last (Fig. 6). This measurement was divided by the number of syllables between these two points to give the mean syllable duration for the echeme. 'Gaps' (momentary breaks in the sound – see Fig. 4) were counted if they occurred during the louder second part of the syllable and were at least 1·25 ms in duration (Fig. 6).

Echeme repetition rate was determined only from periods of *regular* echeme repetition. To put this on an objective basis we used only sequences of four or more echemes during which no two successive intervals between echemes differed from one another by more than 10 per cent of the smaller of the two. The duration of each regular sequence of echemes was measured from the end of the first echeme to the end of the last; the number of echemes included (one fewer than the total number of echemes in the sequence) was then divided by this measurement to give the echeme repetition rate (Fig. 5).

In the field singing usually stops when the sun is hidden by a cloud, and in the studio the lack of radiant heat from a nearby bench lamp usually has a similar effect. If singing does continue in such conditions, the echeme repetition rate is normally much lower and the duration of both the echemes and syllables much greater; the number of gaps per echeme does not change noticeably. Because of this effect we have based our song data only on recordings made when the

Table 1 Data for the field recordings of male calling songs of *Euchorthippus* used in this study. All these recordings were made from different males. Recordings 236/3, 236/4 and 236/6 were made at the type-locality of *E. chopardi*.

Species or subspecies	Locality	Date recorded and collected	Recordist	Shade air temperature	Recording No.
declivus	France: Lozère, near Mende, Col de Montmirat.	10.viii.1977	DRR	21°C	232/2
	France: Vaucluse, Mont Ventoux, road from Bédoin, 1100 m.	12.viii.1977	DRR	18°C	233/6
	France: Alpes-Maritimes, near Col de Vence, 930 m.	25.viii.1977	DRR	25°C	241/1
	France: Alpes-Maritimes, near Col de Vence, 940 m.	10.viii.1982	DRR	23°C	484/4
pulvinatus gallicus	France: Dordogne, near Le Bugue, Campagne.	24.viii.1974	DRR	30°C	134/3
	Same locality	24.viii.1974	DRR	33°C	134/5
	France: Pyrénées-Orientales, St Cyprien.	28.viii.1977	DRR	25°C	136/3
	France: Vaucluse, Mont Ventoux, near Les Bruns.	11.viii.1977	DRR	24°C	232/4
	Same locality	11.viii.1977	DRR	24°C	232/5
	France: Vaucluse, near Carpentras, Bédoin.	13.viii.1977	DRR	22°C	234/8
	Same locality	13.viii.1977	DRR	22°C	235/2
	Spain: Huesca, 5 km NW. of Solsona	9.ix.1978	WJR	27°C	272/3
	Spain: Huesca, 7 km SE. of Seo de Urgel	11.ix.1978	WJR	26°C	272/9
	Same locality	12.ix.1978	WJR	26°C	274/3
chopardi	France: Vaucluse, 3 km SE. of Cavaillon.	14.viii.1977	DRR	27°C	236/3
	Same locality	14.viii.1977	DRR	27°C	236/4
	Same locality	14.viii.1977	DRR	28°C	236/6
	France: Vaucluse, near Carpentras, 3 km S. of Malaucène	15.viii.1977	DRR	23°C	236/8
	Same locality	15.viii.1977	DRR	23°C	236/10
	Spain: Huesca, 8 km. E. of Ainsa	3.ix.1978	WJR	33°C	270/6

insect was in full sunshine or receiving radiant heat from a bench lamp, and we suggest that any recordings compared with our data should be made under similar conditions. Ambient air temperatures are also important, but less so than radiant heat as the insects can regulate their body temperature to some extent by adjusting their orientation to the incident radiation.

When combining the data from the various recordings of each species in order to find the range, overall mean and standard deviation, we treated the mean obtained from each male as an individual observation, thus minimizing the effect of variation in the songs. When comparing a song with our data, it is thus desirable to use mean values taken from as much of the song as possible.

We excluded from our analysis any echemes that were obviously atypical, such as those produced when the insect was just beginning to sing. We based our figures for echeme repetition rate on all the regular sequences in each recording, but the number of echemes used for

Table 2 Data for the studio recordings of male calling songs of *Euchorthippus* used in this study. All these recordings were made from different males except for the following four pairs: (313/4, 316/2), (314/2, 316/1), (179/6, 180/2), (179/9, 180/1).

Species or subspecies	Locality	Date collected	Date recorded	Recordist	Air temperature	Recording No.
declivus	FRANCE: Landes, near Biscarrosse, Millas.	11.ix.1976	12.ix.1976	WJR	20°C	180/3
pulvinatus gallicus	FRANCE: Landes, Arcachon.	13.ix.1976	13.ix.1976	WJR	20°C	180/4
	Same locality	14.ix.1976	15.ix.1976	WJR	18°C	180/8
	SPAIN: Valencia, near Requena, 700 m.	27.vii.1979	30.vii.1979	WJR	25°C	309
	Same locality	27.vii.1979	31.vii.1979	WJR	29°C	313/1
	Same locality	27.vii.1979	31.vii.1979	WJR	27°C	313/2
	Same locality	27.vii.1979	31.vii.1979	WJR	27°C	313/3
	Same locality	27.vii.1979	31.vii.1979	WJR	27°C	314/1
	Same locality	27.vii.1979	31.vii.1979	WJR	27°C	313/4
	Same locality	27.vii.1979	2.viii.1979	WJR	24°C	316/2
	Same locality	27.vii.1979	1.viii.1979	WJR	26°C	314/2
	Same locality	27.vii.1979	2.viii.1979	WJR	27°C	316/1
pulvinatus elegantulus	JERSEY	12.ix.1964	15.ix.1964	J.F.Burton	—	163
	JERSEY: Quennevais.	16.vii.1977	8.viii.1977	WJR	27°C	212
	FRANCE: Loire-Atlantique, 3 km SW. of Guérande.	9.ix.1976	10.ix.1976	WJR	20°C	179/6
	Same locality	9.ix.1976	12.ix.1976	WJR	20°C	180/2
	FRANCE: Loire-Atlantique, near Guérande, Le Croisic.	9.ix.1976	12.ix.1976	WJR	20°C	179/9
	Same locality	9.ix.1976	12.ix.1976	WJR	20°C	180/1
chopardi	SPAIN: Valencia, near Requena, 700 m.	27.vii.1979	30.vii.1979	WJR	27°C	311/1
angustulus	MAJORCA: 1 km W. of Palma Nova.	16–18.ix.1981	21.ix.1981	WJR	29°C	417
	Same locality	16–18.ix.1981	22.ix.1981	WJR	29°C	420

measuring the number of gaps per echeme, echeme duration and syllable duration was generally limited to 50 per recording. When we had two recordings taken from the same male, the mean of each character was calculated separately for each recording and these means were then combined to give a single grand mean for that male.

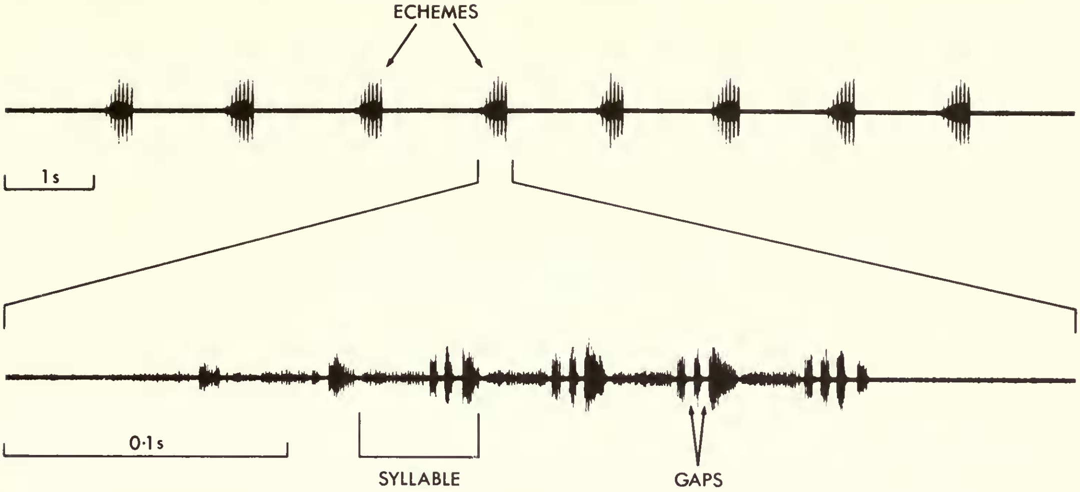
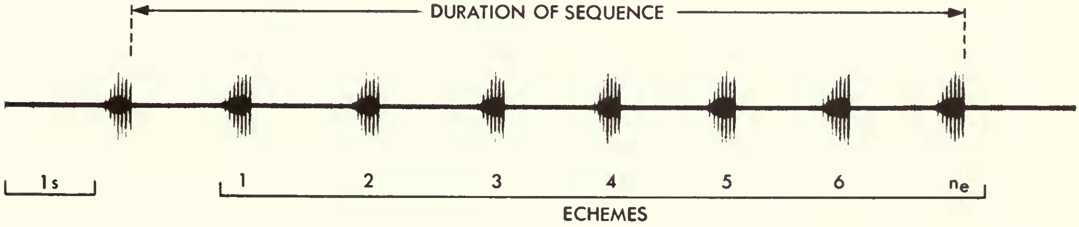
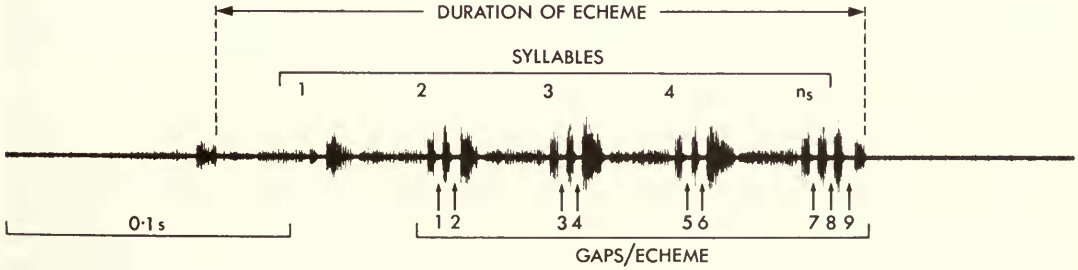


Fig. 4 Oscillograms of the male calling song of *Euchorthippus declivus*, showing the terminology used in this paper.



$$\text{ECHEME REPETITION RATE} = \frac{\text{NUMBER OF ECHEMES } (n_e)}{\text{DURATION OF SEQUENCE}}$$

Fig. 5 Oscillogram of a sequence of echemes from the male calling song of *Euchorthippus declivus*, showing the method of determining the duration of the sequence and the echeme repetition rate.



$$\text{MEAN DURATION OF SYLLABLE} = \frac{\text{DURATION OF ECHEME}}{\text{NUMBER OF SYLLABLES } (n_s)}$$

Fig. 6 Oscillogram of a typical echeme from the male calling song of *Euchorthippus declivus*, showing the method of determining the duration of the echeme, the number and duration of the syllables and the number of gaps per echeme.

Presentation and evaluation of the data

We have chosen to present the morphological and acoustic data in the form of bar-charts (Figs 20, 82–88) because they make it possible to compare at a glance our samples of the taxa and their constituent regional populations. The components of each bar are explained in Fig. 7 (but note that in some bars the range does not extend beyond the standard deviation on one side of the mean). The scale used for each bar-chart was chosen to make the fullest use of the space available, and the resulting differences in scale should be taken into account when comparing the variability of different characters. All morphological measurements are given in millimetres and all temporal ones in milliseconds. For each sample, n represents the number of specimens measured or whose songs have been analysed, and on the bar-charts of acoustic data (Fig. 20) n_e represents the total number of echemes analysed. Where $n<5$ the bar is given as a simple line with no statistical information beyond the range and mean.

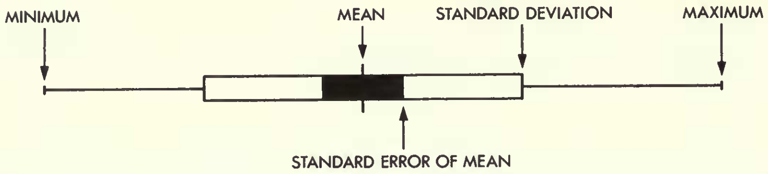


Fig. 7 Diagram explaining the components of the bars used in the bar-charts (Figs 20, 82–88). Note that in some of these bars the range does not extend beyond the standard deviation on one side of the mean and that, when the number of observations is fewer than five, the bar is given as a simple line with no statistical information beyond the range and mean.

We found the bar-charts to demonstrate so clearly and quickly the differences between the taxa, and which characters are most useful in separating them, that we decided it would be pointless to subject the same data to multivariate analysis. We have occasionally applied 't' tests to determine more objectively which of two characters (or combinations of characters) gave the best separation between two taxa, but in every case these did no more than confirm what was obvious from the bar-charts.

The bar-charts also suggested combinations of characters that would give improved separations and we have plotted a selection of these in the form of scatter diagrams (Figs 8–13, 21–24). Fig. 8 shows particularly clearly the contrast in the males between *declivus* and the remaining species in the projection of the fore wing beyond the hind wing. Fig. 9 gives a complete separation of the males of *declivus, pulvinatus* and *chopardi*, especially if the French samples are considered alone. Figs 10 and 11 achieve a similar result for both sexes, but the French and Spanish samples have to be considered separately in order to obtain a complete separation in the males. Figs 21–24 show rather more clearly than the acoustic bar-charts (Fig. 20) the difference between the songs of *declivus, pulvinatus* and *chopardi*.

The best morphological separation between males of *declivus, pulvinatus* and *chopardi* was achieved by plotting three characters as percentages on a triangular graph (Fig. 12). The procedure for this is described by Mayr (1969) and is best explained by an example. For one specimen the following figures were obtained: number of stridulatory pegs 148, length of pronotum/length of head 1·09 and distance of stigma from tip of fore wing 2·68 mm. Since the figures for the last two characters are small compared with the first, they were multiplied by 100 and 25, respectively. The three figures used were thus 148, 109 and 67, giving the sum 324. The three characters represent 45·7 per cent, 33·6 per cent and 20·7 per cent of their sum and these percentages were used to enter a single point on the graph, the axes being arranged so that the sum of the three coordinates of each point was always 100. The graph thus shows proportions rather than absolute sizes.

Figure 12 gives perhaps the most convincing demonstration that *declivus, pulvinatus* and *chopardi* do not constitute a single, continuously variable species, though it does not of course

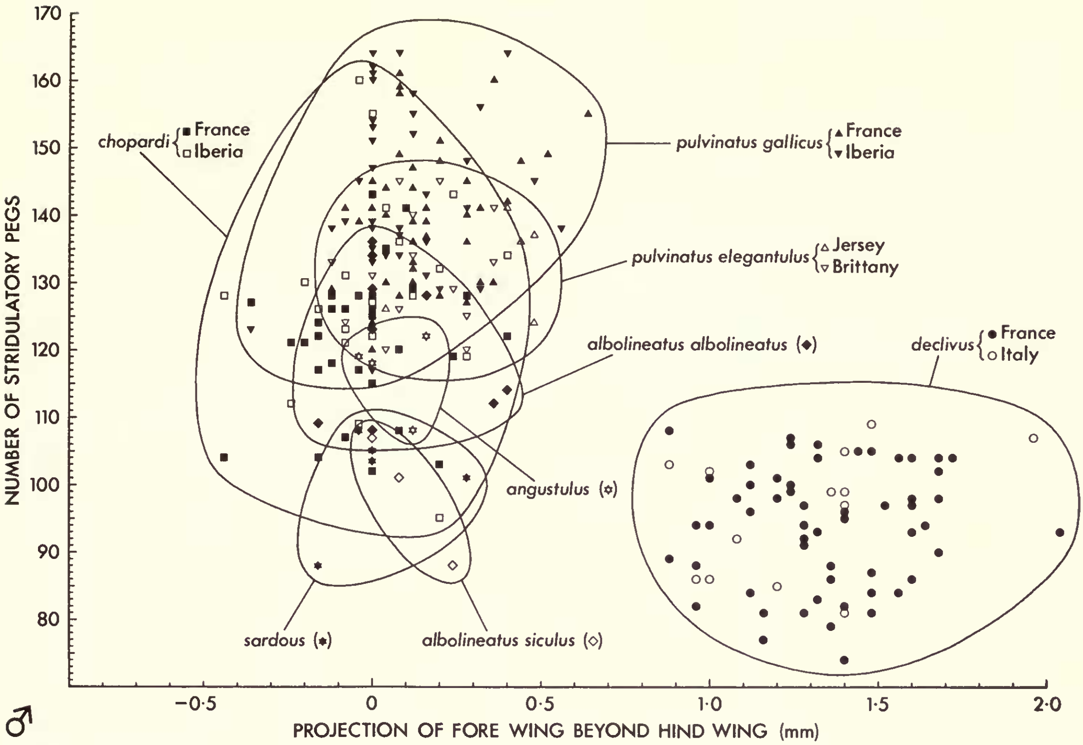


Fig. 8 Scatter diagram showing a plot of the number of stridulatory pegs against the projection of the fore wing beyond the hind wing in males of *Euchorthippus*. The negative values on the horizontal axis are for specimens in which the hind wing projects beyond the fore wing.

rule out polymorphism. Figure 13 shows that, using the same combination of characters, *albolineatus* and *angustulus* resemble *chopardi*, while *sardous* is nearer to *pulvinatus*.

It should be noted that in some scatter diagrams the number of points entered is smaller than the number of specimens measured (as shown in the bar-charts), because in a few specimens *both* (or, in the case of the triangular graphs, *all four*) of the characters were not available. Where two different population symbols would have coincided exactly, only one symbol is shown in the morphological scatter diagrams; the symbol chosen is the one considered to be more useful or informative (e.g. near the edge of the cluster concerned). In the song scatter diagrams (Figs 21–24), for which fewer points were available, coincident symbols have been moved apart slightly so that both can be seen.

Characters studied

Morphology

We have concentrated on morphological characters that are easy to use with pinned specimens and have therefore excluded those characters of the fore wing that are often hidden behind the hind legs (e.g. the width of the medial and cubital areas) or are difficult to measure without opening and flattening the wings (e.g. the width of the fore wing). We have also tried to avoid characters that tend to change as the body shrinks after death, and have therefore used the length of the hind femur as a measure of size in preference to body length, which is often greatly altered by post mortem shrinkage (and in the females is also much influenced by gravidity). We have, however, included the lengths of the male subgenital plate and abdominal tergites 9+10 because of the emphasis placed on these measurements by Descamps (1968), although we have

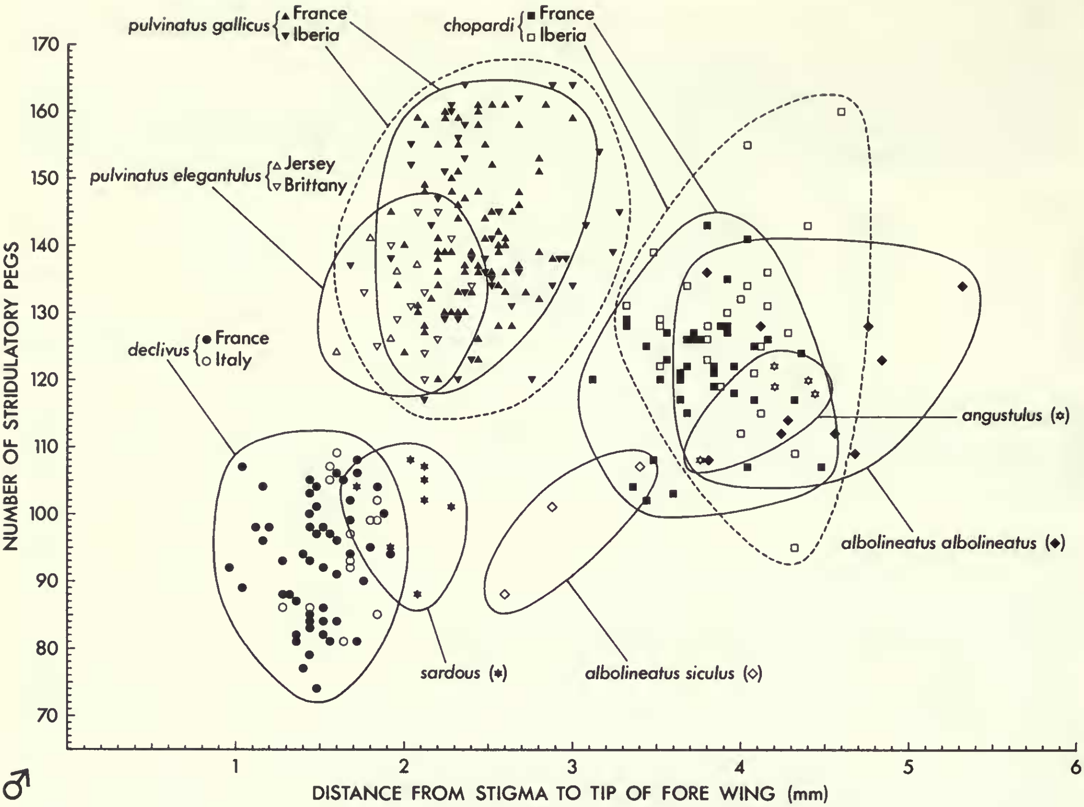


Fig. 9 Scatter diagram showing a plot of the number of stridulatory pegs against the distance from the stigma to the tip of the fore wing in males of *Euchorthippus*. To facilitate comparison broken lines are used for the two Iberian samples.

found that their usefulness is much reduced by shrinkage during drying. We suspect that the distance by which the fore wing projects beyond the hind wing is also affected by post mortem shrinkage, but this does not prevent it from being a useful character.

Head and pronotum

The lengths of the head and pronotum are not very useful taxonomic characters other than as measures of size or when taken as a ratio of one to the other. This ratio is frequently useful for separating *chopardi* from the other mainland species and was used by Descamps (1968) to distinguish *chopardi* from *angustulus, albolineatus albolineatus* and *a. siculus*. However, the pronotum/head ratios of Iberian *chopardi* show a large overlap with those of the other taxa (Figs 82, 86).

The prominence of the median and, especially, lateral carinae of the pronotum is often useful in distinguishing between species, but this character is rather difficult to use until one is familiar with the differences shown. We have attempted to show in diagrammatic cross-section (Figs 31–34) the degree of prominence of these carinae in *declivus, pulvinatus gallicus, chopardi* and *albolineatus albolineatus*. Figures 31–39 also show dorsal views of the pronotum of males of all the taxa dealt with in this paper. In most species the lateral carinae are almost straight but in *sardous* they are distinctly incurved in the prozona (Fig. 38). They are also somewhat incurved in *angustulus*, but less so in specimens from Majorca than in those from Formentera.

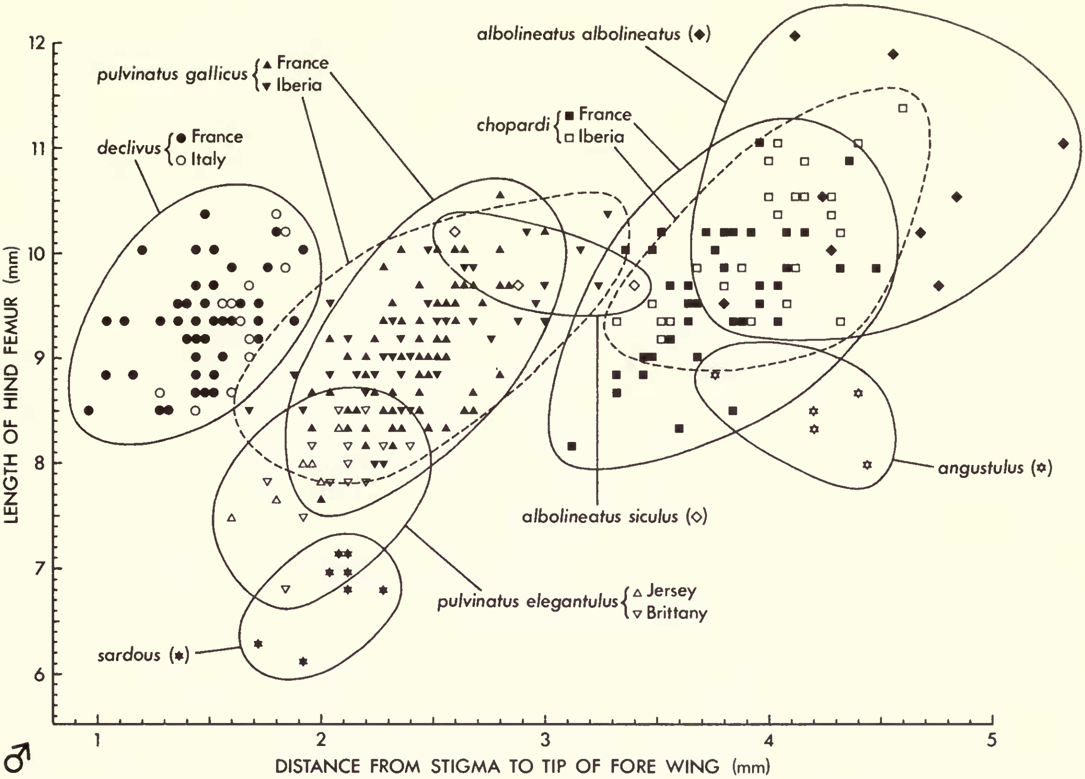


Fig. 10 Scatter diagram showing a plot of the length of the hind femur against the distance from the stigma to the tip of the fore wing in males of *Euchorthippus*. To facilitate comparison broken lines are used for the two Iberian samples.

Fore wing

The absolute and relative lengths of the fore wing are useful characters and have been much used by previous authors (e.g. Defaut, 1982). The position of the tip of the fore wing in relation to the hind knee or, less reliably, the apex of the abdomen provides one of the easiest methods of distinguishing between typical *declivus, pulvinatus gallicus* and *chopardi* in the field (Figs 25–30). The length of the fore wing is more useful when taken as a ratio with the length of the hind femur; this is particularly true in the female, in which the range of our sample of *p. gallicus* does not overlap with those of *chopardi* or *a. albolineatus* (Fig. 87).

The fore wings are short in *declivus* and become progressively longer in both sexes in the sequence *declivus, p. gallicus, chopardi* and *a. albolineatus* (Figs 83, 87).

The distance from the stigma to the tip of the fore wing is, to some extent, proportional to the length of the fore wing but provides an even better character, especially when used as a ratio with the length of the hind femur (Figs 84, 85, 88). When these two characters are plotted against each other in a scatter diagram, there is no overlap in our male samples of the populations of the three species occurring in France (*declivus, pulvinatus* and *chopardi*) or between the two occurring commonly in Spain (*pulvinatus* and *chopardi*) (Fig. 10). In females there is no overlap at all between our samples of *declivus, pulvinatus* and *chopardi* (Fig. 11), though *a. albolineatus* is very closely associated with *chopardi* in both sexes. *E. p. elegantulus* agrees with *p. gallicus* rather than with *declivus* when the measurements are plotted against the length of the hind femur (Figs 10, 11) or, in males, against the number of stridulatory pegs (Fig. 9).

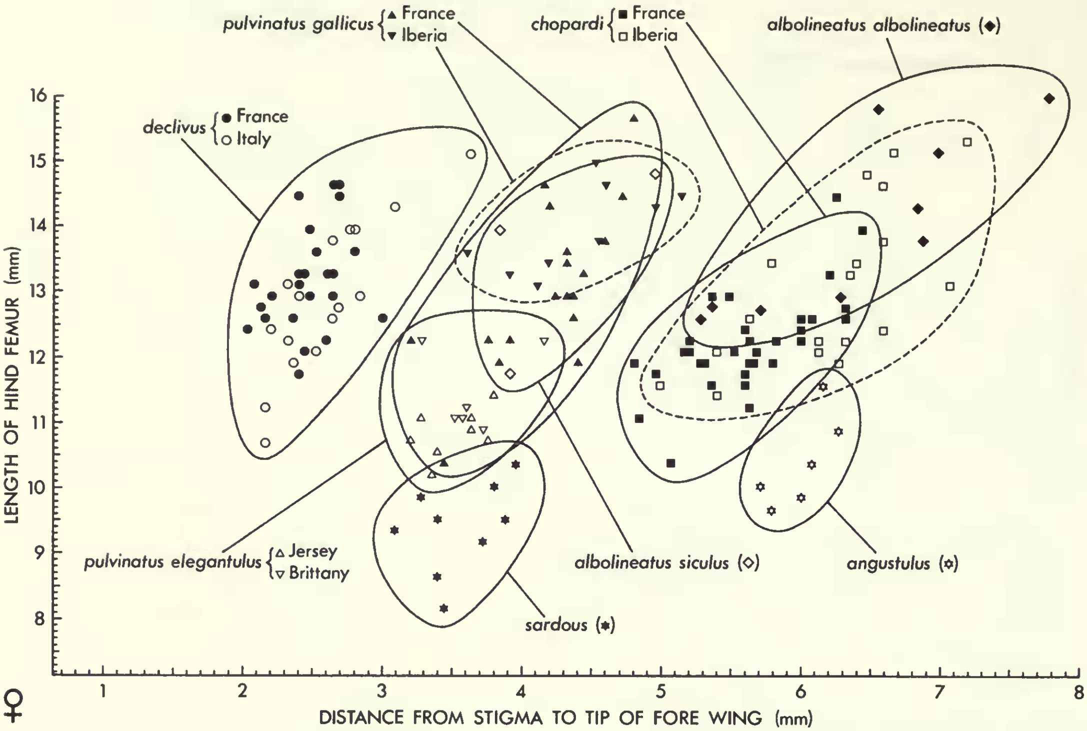


Fig. 11 Scatter diagram showing a plot of the length of the hind femur against the distance from the stigma to the tip of the fore wing in females of *Euchorthippus*. To facilitate comparison broken lines are used for the two Iberian samples.

Hind wing

The length of the hind wing is often a useful character (Figs 83, 87), especially when taken as a ratio with the length of the hind femur (Figs 84, 87). In this ratio, for both sexes, *p. elegantulus* is again closer to *p. gallicus* than to *declivus*, which is distinct from all the other taxa. In the female this character separates *chopardi* from *p. gallicus*.

Projection of the fore wing beyond the hind wing

The distinct gap between the tips of the flexed fore and hind wings provides the best character for distinguishing *declivus* from the remaining taxa (Figs 8, 84, 88). This character has been mentioned by several authors (Chopard, 1952; Descamps, 1968; Harz, 1975; Luquet, 1978; Defaut, 1982) but its significance in showing that *elegantulus* is distinct from *declivus* has not been previously realized (see p. 132).

Hind femur

The length of the hind femur (Figs 82, 86) is useful only as a measure of size, for which purpose we have used it in ratios with the length of the fore wing, the length of the hind wing and the distance from the stigma to the tip of the fore wing (Figs 10, 11, 84, 85, 87, 88).

Stridulatory file

Counting the stridulatory pegs takes at least a minute per specimen and ideally requires a microscope with a movable stage. We have found the effort worthwhile, however, as this character, in combination with stigma distance and pronotum/head ratio on a triangular graph,

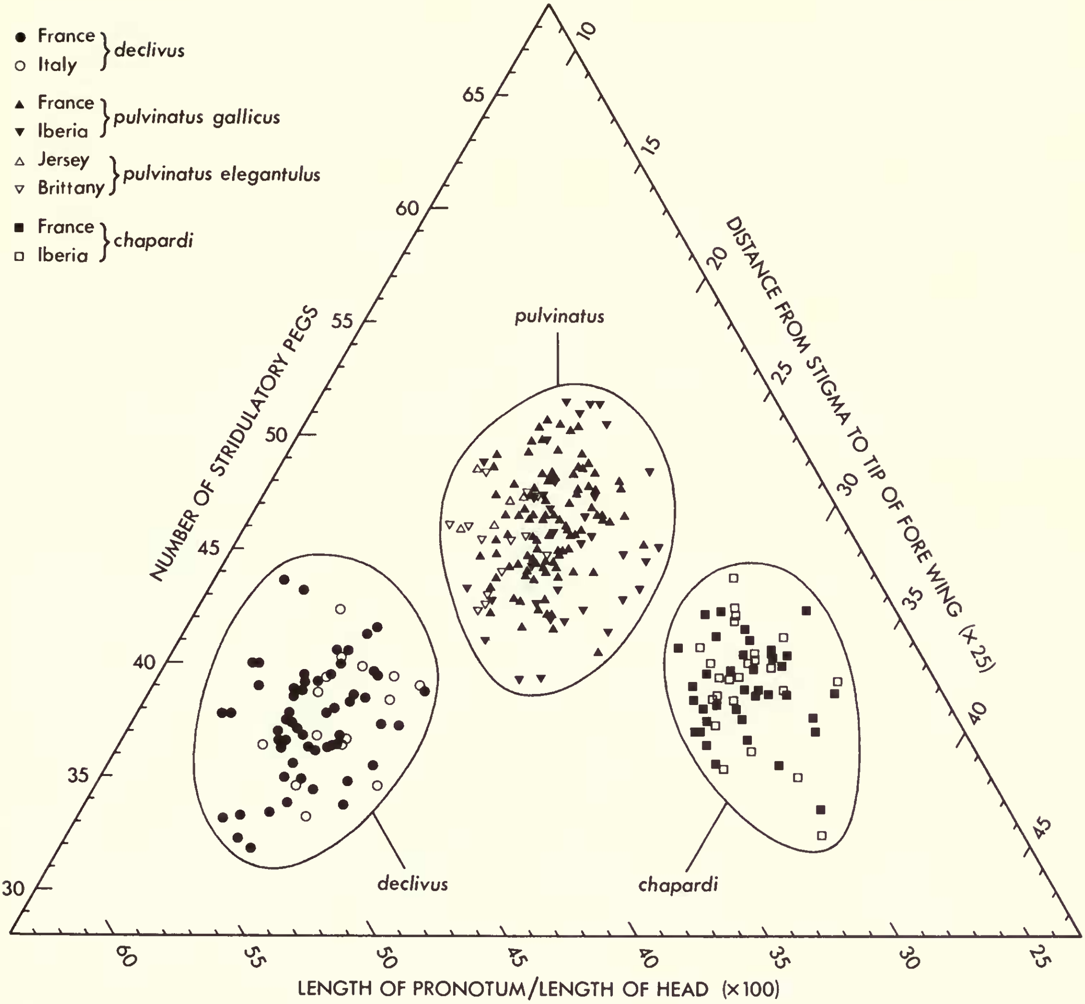


Fig. 12 Triangular graph showing the relationship between males of *Euchorthippus declivus, E. pulvinatus* and *E. chopardi* as determined by three diagnostic characters. (See the text for full explanation.)

has provided one of the best means of separating males of *declivus, pulvinatus* and *chopardi* (Fig. 12). The first two of these characters give almost as good a separation in a two-axis scatter diagram (Fig. 9). The stridulatory pegs provide another character showing the close relationship between *p. elegantulus* and *p. gallicus* (Fig. 83). *E. p. elegantulus* has, on average, slightly fewer pegs than *p. gallicus*, as would be expected from the difference in size, but in both of the two-axis scatter diagrams and in the triangular graph *p. elegantulus* is clearly more closely associated with *p. gallicus* than with *declivus*.

We have found it necessary to examine the female stridulatory pegs only in order to find the best means of separating *a. siculus* and *pulvinatus*. The pegs are smaller in females and are more likely to be replaced by hairs, but it is still usually possible to count them by viewing the file in profile. In cases where this is difficult a replica of the file can be made (see Pitkin, 1976).

We did not find the length of the stridulatory file to be a useful character, the very short file of *sardous* simply reflecting the generally small size of this species and in particular its short hind femora (cf. Figs 82 and 83).

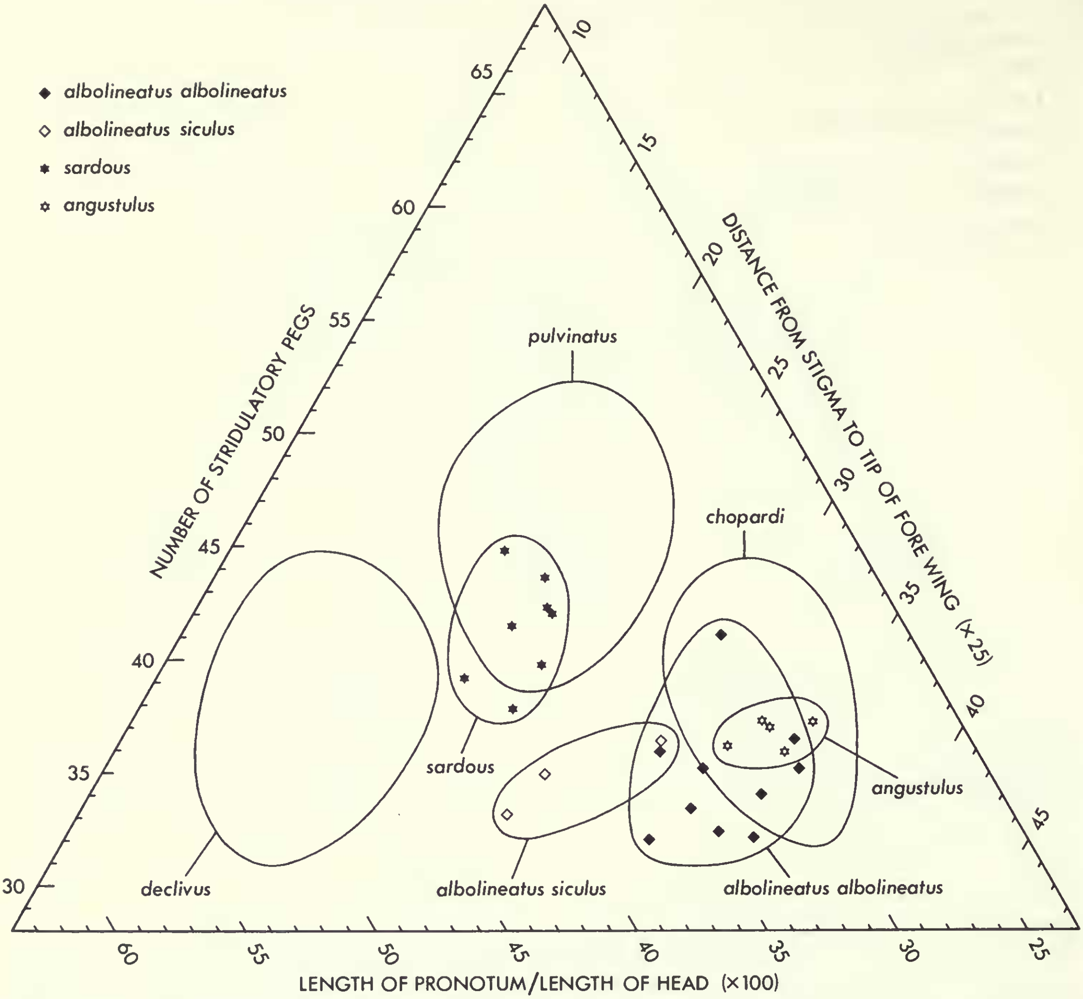


Fig. 13 Triangular graph showing the relationship between males of *Euchorthippus* as determined by three diagnostic characters. The detailed plots for *E. declivus, E. pulvinatus* and *E. chopardi* are shown in Fig. 12. (See the text for full explanation.)

Male subgenital plate and abdominal tergites 9+10

The shape of the male subgenital plate has been used as a key character by all previous authors. Descamps (1968) tried to make this character more objective by comparing the length of the subgenital plate with that of abdominal tergites 9+10, and concluded that in *declivus* and *pulvinatus* the dorsal part of the subgenital plate was longer than abdominal tergites 9+10 in profile, while in *chopardi, a. albolineatus, a. siculus, angustulus* and *sardous* these tergites were longer than, or subequal to, the subgenital plate.

We have found that measuring the subgenital plate accurately in dried specimens is difficult, since post mortem shrinkage may cause the proximal end of the subgenital plate to be covered by the supra-anal plate. Another problem is caused by the way in which variation in the degree of curvature of the abdomen affects the measurement of the length of tergites 9+10. Perhaps partly because of these difficulties, we have not found the ratio of the length of the subgenital plate to that of abdominal tergites 9+10 to be particularly useful; for *declivus* and *p. gallicus* the ratio is in fact less useful than the length of the subgenital plate alone (Fig. 85).

We have found the shape of the male subgenital plate to be more useful than its dimensions. It is always distinctly pointed in *declivus*, bluntly rounded in *chopardi* and intermediate in *pulvinatus* (Figs 25, 27, 29), but without some experience of the group it is easy to be misled by this character. The frequent misidentification of Spanish *p. gallicus* as *declivus* has doubtless been the result of using the male subgenital plate as the principal distinguishing character.

Internal male genitalia

We have examined the internal male genitalia of all the species included in this study and have found no taxonomically useful character.

Colour pattern

Most specimens show some degree of dark longitudinal striping, especially on the head, and in *chopardi* these stripes are particularly conspicuous (Fig. 40). We have seen a few conspicuously striped specimens that seem to be *pulvinatus* on other characters, but well-developed stripes of the kind shown in Fig. 40 are characteristic of *chopardi*.

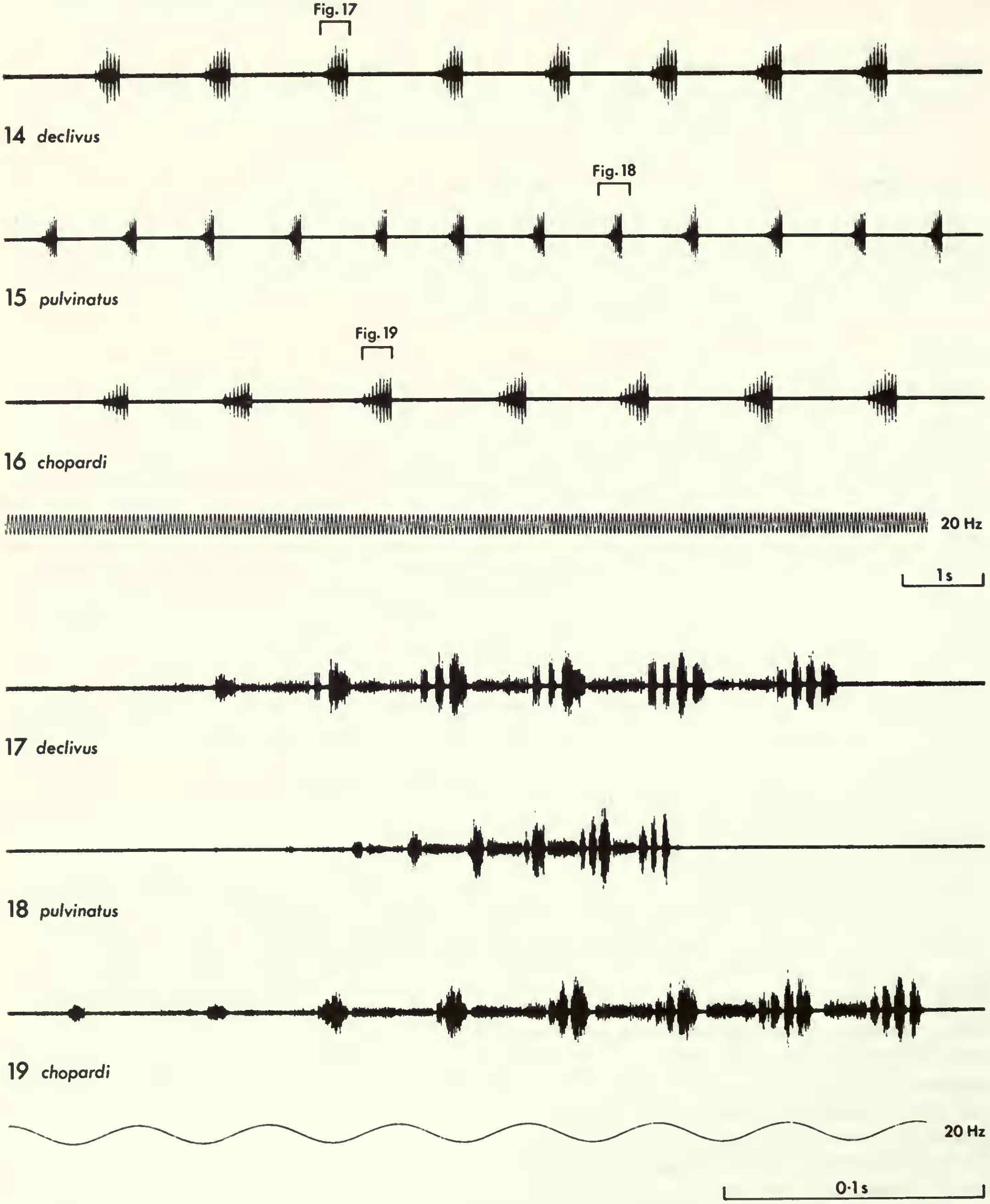
Cytology

In common with other Gomphocerinae of the *Chorthippus*-group, the species of *Euchorthippus* in which the chromosomes have been studied have complements of 17 in the male (XO) and 18 in the female (XX) (Hewitt, 1979, Santos *et al.*, 1983). The chromosomes of *pulvinatus* have been examined by McClung (1932), Arana *et al.* (1980), Ferrer *et al.* (1981), Santos & Giráldez (1982) and Santos *et al.* (1983), while those of *albolineatus* have been described by Carlson (1936) (Carlson's specimens were identified by Hebard as *pulvinatus*, but as they came from Algeria they were almost certainly *albolineatus*, the only species of *Euchorthippus* known to occur in North Africa). Santos *et al.* (1983) have also examined the chromosomes of Spanish *chopardi* and have shown that the C-banding patterns differ quite markedly from those of Spanish *pulvinatus* (these authors refer to *chopardi* as '*albolineatus*', but Dr Santos has kindly shown us the specimens and we consider them to be *chopardi*). Although the number and gross morphology of the chromosomes are likely to be uniform throughout the genus, it would clearly be interesting to study the C-banding patterns in other species; careful comparison may also reveal differences in chiasma frequency, relative lengths of chromosomes or DNA content of equivalent nuclei (John & Hewitt, 1966; White, 1972).

Santos *et al.* (1983: 73) have succeeded in rearing artificial hybrids between *pulvinatus* and *chopardi*. This raises the possibility of natural hybrids occurring between these species, which quite often occur together. We have seen a few specimens that are intermediate between the two in some morphological characters, but in order to recognize natural hybrids with any confidence it would be necessary to investigate them genetically and, in the case of males, to analyse the calling song.

Song

There has been no comprehensive study of the acoustic behaviour of *Euchorthippus*, but several authors have published comments on the songs of one or more species. Chopard (1952) briefly outlined the calling song of *pulvinatus* and Faber (1953) described its complete acoustic repertoire, including calling, courtship and rivalry songs. Descamps (1968) published oscillograms of one echeme each of *declivus, pulvinatus* and *chopardi*, but found no noticeable difference between them and gave a single description of the calling and courtship songs for all three species. Luquet (1978) gave a diagram of one echeme for each of these species and suggested that the echeme was longest in *declivus*, almost as long in *chopardi* and shortest in *pulvinatus* (our own analyses, however, show the echemes to be longer in *chopardi* than in *declivus* – see Fig. 20). Luquet also found that *pulvinatus* had a more rapid 'cadence' (? echeme repetition rate) than the other two species, but he considered these differences to be insufficient to permit identification in the field. Schmidt & Schach (1978) gave oscillograms of the courtship song of *pulvinatus* and *declivus*, and described differences in the duration of the syllables and echemes, but neither these authors nor any others have seriously suggested using the song as a taxonomic character.



Figs 14–19 Oscillograms of typical male calling songs of (14, 17) *Euchorthippus declivus*, (15, 18) *E. pulvinatus* and (16, 19) *E. chopardi*. Figs 17–19 are faster oscillograms of the single echemes indicated in Figs 14–16. The oscillograms were taken from recordings 233/6, 232/4 and 236/8, for which full information is given in Table 1 (p. 107).

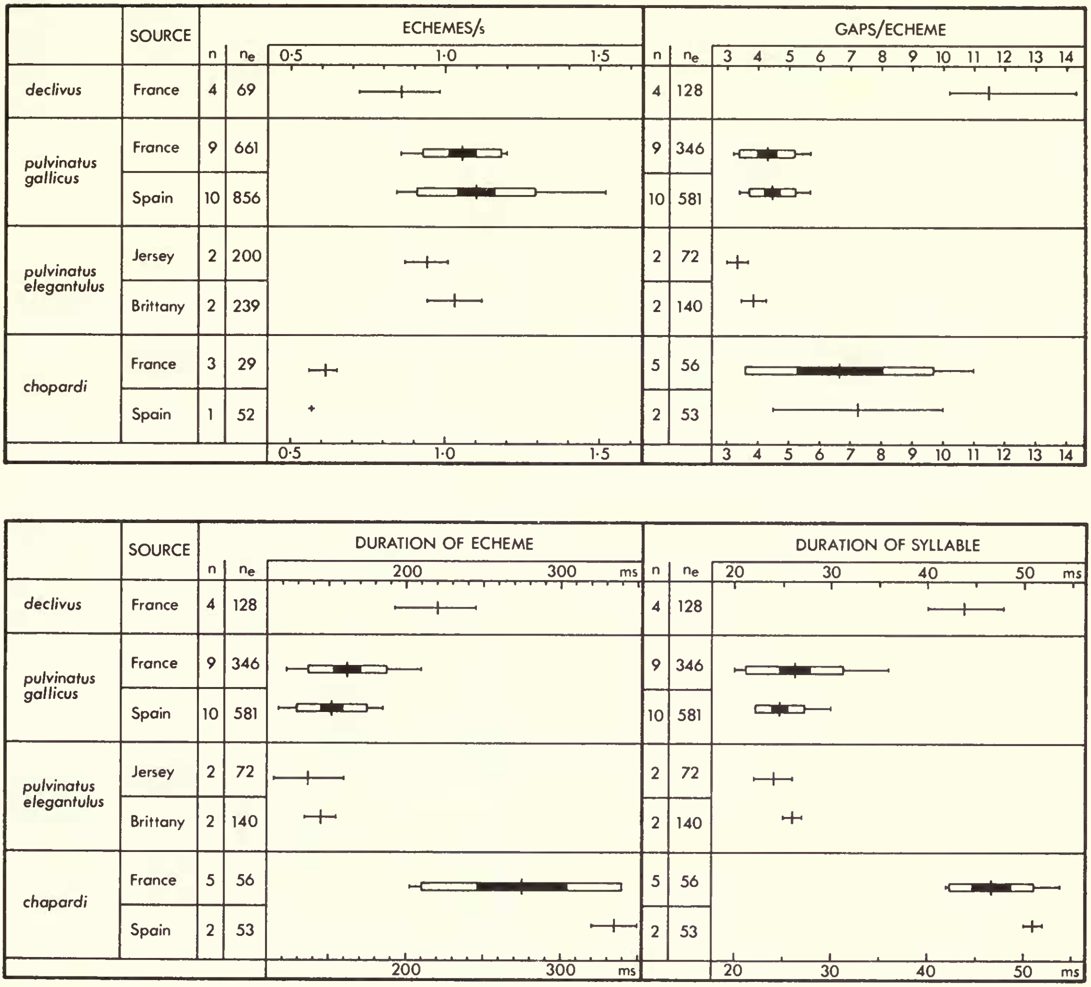
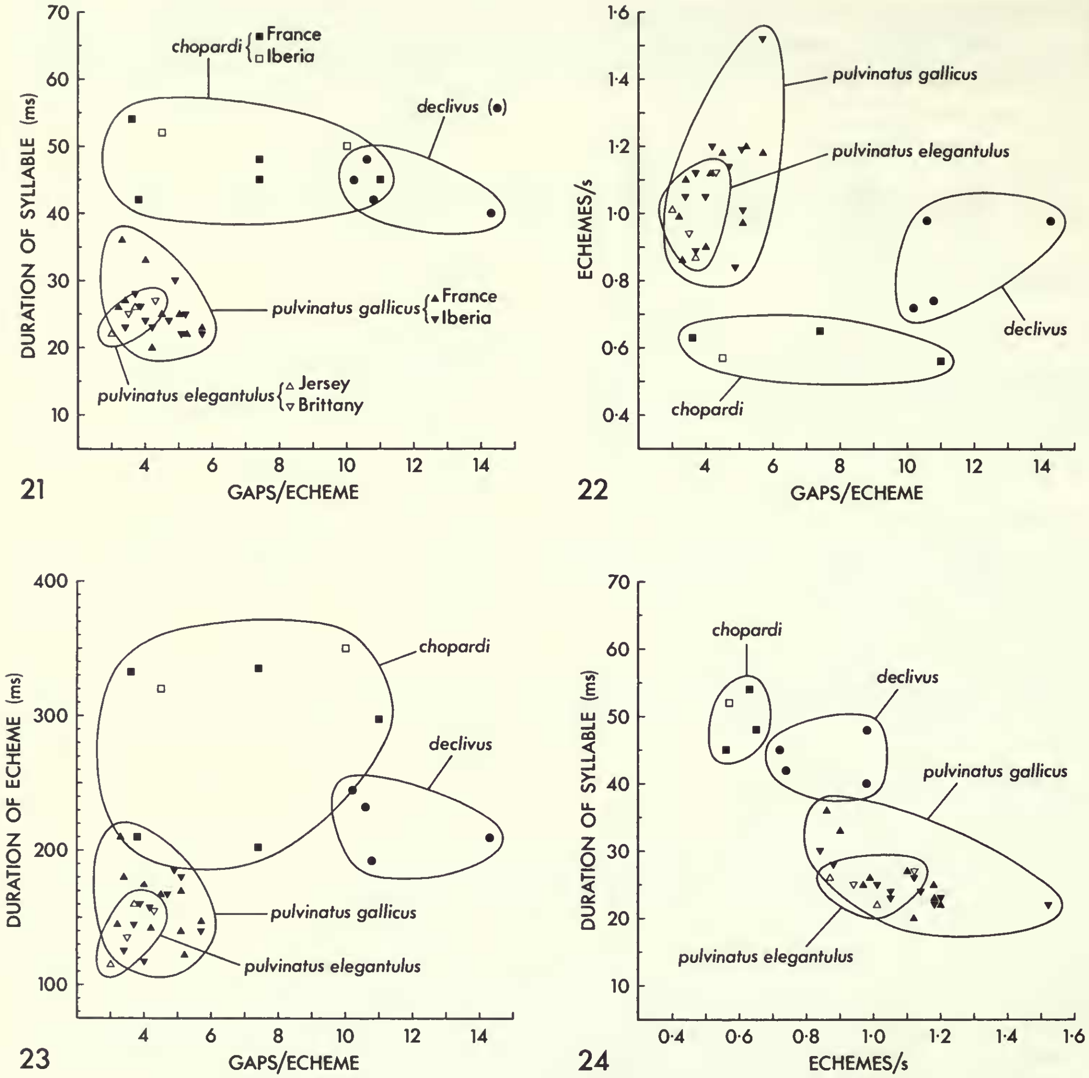


Fig. 20 Data for four characters of the male calling songs of *Euchorthippus declivus, E. pulvinatus* and *E. chopardi*. For explanation of the bars see Fig. 7; n = number of males, n_e = number of echemes from which data were taken. Note that in compiling these charts the *mean* values obtained from each male were treated as individual observations. (For further explanation see p. 110.)

While our own observations are broadly in agreement with those of these authors, our more detailed analyses have revealed good, taxonomically useful differences between the songs of *declivus, pulvinatus* and *chopardi*. Figures 14–19 show oscillograms of typical sequences of echemes from the male calling songs of these three species, followed by much faster oscillograms of single echemes selected from these sequences. The full data from all our recordings are given in Fig. 20 and scatter diagrams from four selected pairs of song characters are shown in Figs 21–24. The most striking difference is between the large number of gaps per echeme in *declivus* and the much smaller number in *pulvinatus*. This difference has not previously been observed although it is clearly visible in the oscillograms given by Descamps (1968: Fig. 23 – but note that the oscillogram for *declivus* is shown backwards). The number of gaps per echeme in *chopardi* is also lower than in *declivus*, but the difference is less striking and our recordings of *chopardi* show a high degree of variability in this character. Both the syllables and echemes are of shorter duration in *pulvinatus* than in *declivus*, the syllables showing the clearer contrast (Fig. 20). In all these characters the bar-charts and scatter diagrams show a close association between *p. gallicus* and *p. elegantulus* (Figs 20–24).



Figs 21–24 Scatter diagrams showing plots of four pairs of characters of the male calling songs of *Euchorthippus declivus, E. pulvinatus* and *E. chopardi*. Note that each point represents the *mean* values of the two characters obtained from one male. The symbols are explained in Fig. 21.

None of these differences in song can be measured without the help of recording and analysing equipment – indeed the gaps, which last for little more than a millisecond, are quite undetectable by the unaided human ear (though being easily resolved by the insects themselves – see, for example, the review of Autrum, 1963). The only song character that can be used as an aid to field identification is the echeme repetition rate, which can be quite easily measured using the second hand (or digital count) of a wrist-watch. As shown in Fig. 20 this character does not show striking contrasts between the species but, when they are singing in similar warm, sunny conditions, *chopardi* has a slower rate than the other two, and *pulvinatus* usually has a faster rate than *declivus*.

It should be emphasized that, for taxonomic use, measurements of all these characters should be based on as many echemes as possible and should always be taken from songs produced by *isolated* males singing in warm sunshine (or in a warm laboratory with a source of radiant heat).

The echeme repetition rate should be based only on *regular* sequences of echemes (see p. 106) and, for each male, it is the *mean* values of all these song characters that should be compared with the bar-charts and scatter diagrams (Figs 20–24).

The number of syllables in each echeme (usually 6–7, occasionally 5 or 8) appears to have little or no taxonomic value. We counted the syllables in the course of calculating the syllable duration, and it soon became clear that intraspecific variation would obscure any trend towards an interspecific difference.

EUCHORTHIPPUS Tarbinskii

Euchorthippus Tarbinskii, 1925: 192; Uvarov, 1926: 341 [redescription]. Type-species: *Oedipoda pulvinata* Fischer de Waldheim, by original designation.

Sinhippus Ramme, 1939: 132. Type-species: *Sinhippus alini* Ramme [= *Euchorthippus unicolor* (Ikonnikov)], by original designation. [Synonymized by Bei-Bienko & Mishchenko, 1951: 543.]

Diagnosis. ♂♀. Fastigium of vertex rather rounded and relatively blunt; foveolae rather short and shallow, each with weak carinula leading inwards and backwards from its posterior end. Antennae not clubbed. Lateral carinae of pronotum straight or slightly incurved. Pleura coarsely rugose and punctate. Inner and outer tarsal claws of different lengths. Brachypterous to macropterous. Precostal area of fore wings with small bulge on anterior margin; medial area not conspicuously widened, without intercalary vein and with irregular cross-veins. Hind wings transparent and colourless. Subgenital plate bluntly to acutely conical. Ovipositor short, without lateral teeth. General coloration brown, straw-coloured or grey (sometimes with greenish tinge but never clearly green or reddish in western European species), with longitudinal dark and light stripes on head and sometimes pronotum. Female usually with white linea scapularis.

Male calling song. In the four species whose stridulation we have studied (*declivus, pulvinatus, chopardi* and *angustulus*) the calling songs have the same basic structure though differing in detail (Fig. 4). They consist of a sequence of echemes repeated at a rate of 0·5–1·5 per second for an indefinite period, sometimes a minute or more. Oscillographic analysis shows that each echeme begins quietly, lasts about 150–350 ms and is composed of 5–8 syllables, each of which has a quiet first part and a louder second part; in at least the later part of each echeme, the louder second part of each syllable contains momentary breaks in the sound, referred to in this paper as 'gaps' (Fig. 4).

Discussion. *Euchorthippus* is an easily recognized genus to the experienced acridologist, but its morphological diagnostic characters are rather subtle and difficult to describe. In comparison with *Chorthippus*, with which it is most easily confused, *Euchorthippus* has a more elongate head when viewed from the side, with the eyes produced anterodorsally into a more pronounced and acute angle. The foveolae are rather weakly (sometimes very weakly) developed, and from the posterior end of each one arises a feeble carinula, usually extending inwards and backwards towards the mid-line of the head, where there is often another feeble median carinula, especially on the fastigium; these carinulae are quite absent in *Chorthippus*. The difference in size between the inner and outer tarsal claws has been used by some authors as a key character, but there is sometimes a tendency towards this size difference in *Chorthippus*. The western European species of *Euchorthippus* are always brown, straw-coloured or grey and, although sometimes showing a greenish tinge, never have the clear green or reddish colours common in *Chorthippus* and other Gomphocerinae.

The calling song of the male provides a particularly good character for recognizing *Euchorthippus* in the field. The long sequences of rapidly repeated echemes are highly characteristic and quite unlike the songs of any other European Gomphocerinae we have heard. Some other Gomphocerinae (e.g. *Chorthippus parallelus* (Zetterstedt), *C. montanus* (Charpentier), *C. dorsatus* (Zetterstedt), *C. dichrous* (Eversmann), *Chrysochraon dispar* (Germar)) have calling songs composed of long sequences of echemes, but in all these cases the repetition rate is much lower, never higher than one every two seconds. The echeme-sequences of *Euchorthippus* are in fact more strongly reminiscent of those produced by some Tettigoniidae, especially such Decticinae as *Metrioptera brachyptera* (L.), *Platycleis sabulosa* Azam and *P. albopunctata* (Goeze), all of which are at least partially diurnal singers; *P. sabulosa* even has a similar number of syllables per echeme (usually 6–7), but all these species have a higher echeme repetition rate when singing during the day, usually more than 2 echemes/s in warm sunshine. Although isolated males of *Euchorthippus* can maintain a fairly regular echeme repetition rate for quite long periods, they never quite achieve the almost mechanical regularity and very long duration (often many minutes) of the echeme-sequences of these Decticine bush-crickets.

There is no elaborate courtship song but in the presence of a female the male produces a somewhat modified song in which the echemes are quieter and the sequences longer than usual. Faber (1953) described a second stage in the courtship song of *pulvinatus* in which there is a gradual increase in the intensity, repetition rate and duration of the echemes, and in the number of syllables per echeme. Just before jumping on to the female, the male produces two or three quiet sounds, each consisting of one or two syllables, and then one loud and more extended sound of uniform intensity.

DISTRIBUTION. Southern Europe, most of the larger Mediterranean islands, Madeira, North Africa and temperate Asia as far as China.

INCLUDED SPECIES. *E. albolineatus* (Lucas), *E. angustulus* Ramme, *E. arabicus* Uvarov, *E. chenbaensis* Tu & Cheng, *E. cheui* Hsia, *E. chopardi* Descamps, *E. declivus* (Brisout), *E. madeirae* Uvarov, *E. pulvinatus* (Fischer de Waldheim), *E. sardous* Nadig, *E. transcaucasicus* Tarbinskii, *E. unicolor* (Ikonnikov), *E. weichowensis* Chang, *E. yungningensis* Cheng.

Key to the western European and North African species and subspecies of *Euchorthippus*

The two mainland taxa *pulvinatus gallicus* and *chopardi*, both common in southern France and the Iberian Peninsula, are particularly difficult to distinguish from each other, and for reliable identification of specimens from these regions (even including females thought to be *declivus*) we recommend taking the relevant measurements and plotting them on the scatter diagrams shown in Figs 10 and 11. For males the use of the triangular graph shown in Fig. 12, although requiring more effort, will produce an even more reliable result.

1 Fore wings projecting beyond hind wings (when flexed) by at least 0·8 mm in ♂, usually at least 0·5 mm in ♀. Male subgenital plate long and pointed, as in Fig. 25. Distance from stigma to tip of fore wing usually less than 0·21 times length of hind femur in ♂, less than 0·25 in ♀ .... **E. declivus** (Brisout) (p. 125)

– Fore wings not projecting beyond hind wings (when flexed) or projecting by less than 0·7 mm in ♂, usually less than 0·5 mm in ♀. Male subgenital plate shorter or less pointed, as in Figs 27 or 29. Distance from stigma to tip of fore wing usually more than 0·21 times length of hind femur in ♂, more than 0·25 in ♀ 2

2 Pronotal lateral carinae distinctly incurved in prozona (Fig. 38); length of pronotum less than 2·1 mm in ♂, less than 3·0 mm in ♀. (Sardinia only) .... **E. sardous** Nadig (p. 136)

– Pronotal lateral carinae straight or almost so in prozona; length of pronotum more than 2·1 mm in ♂, more than 3·0 mm in ♀. (Not known from Sardinia) 3

3 Male subgenital plate relatively short and blunt, as in Fig. 29. Fore wings long, reaching at least base of genicular lobes of hind femora in both sexes. Distance from stigma to tip of fore wing usually more than 0·34 times length of hind femur in ♂, more than 0·38 in ♀ 4

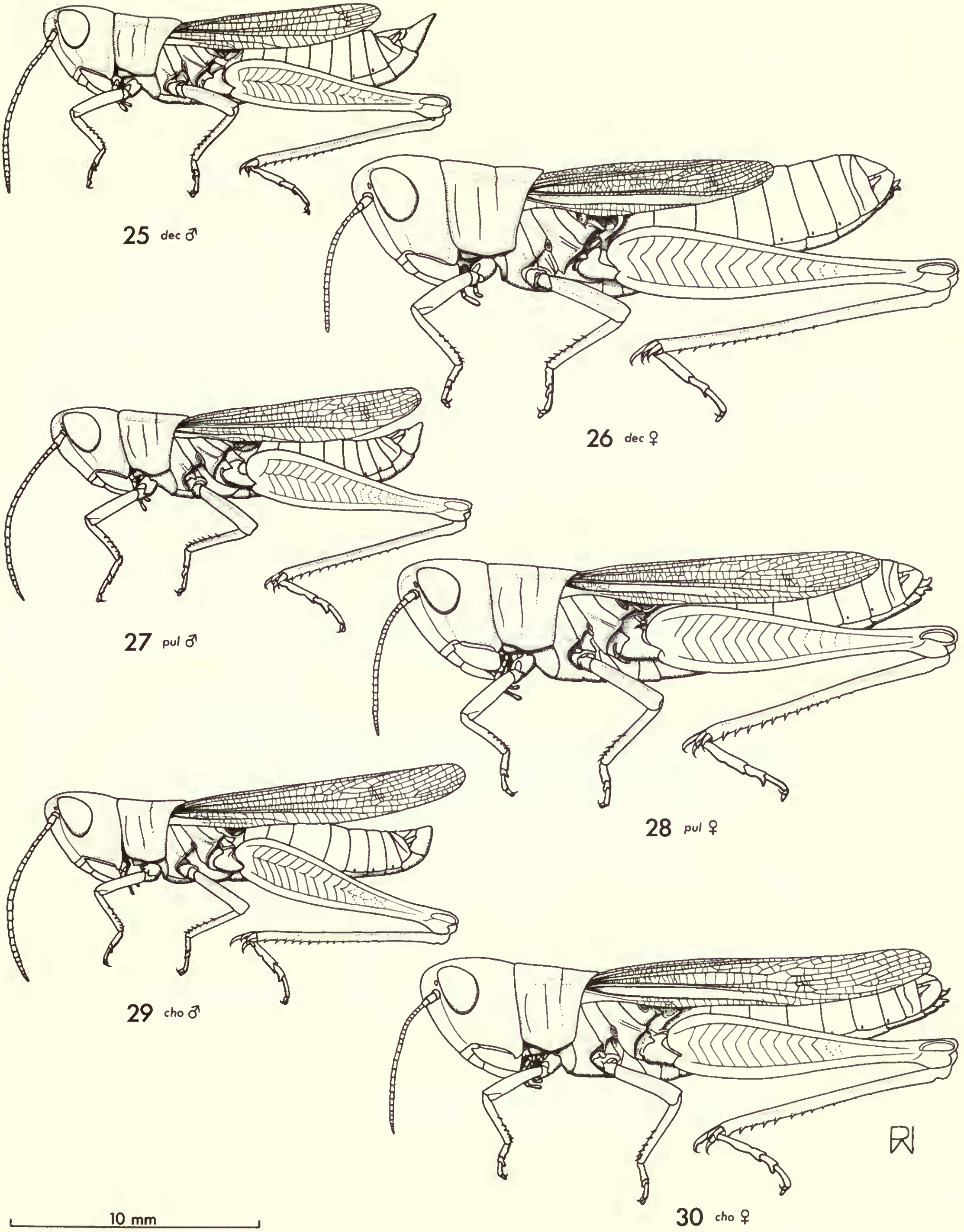
– Male subgenital plate longer and slightly pointed, as in Fig. 27. Fore wings shorter, in female not reaching base of genicular lobes of hind femora. Distance from stigma to tip of fore wing usually less than 0·34 times length of hind femur in ♂, less than 0·38 in ♀ 6

4 Known only from southern France and the Iberian Peninsula. Pronotal lateral carinae relatively low and broad, as in Fig. 33. Head and pronotum usually with conspicuous dark and light longitudinal stripes (Fig. 40) .... **E. chopardi** Descamps (p. 133)

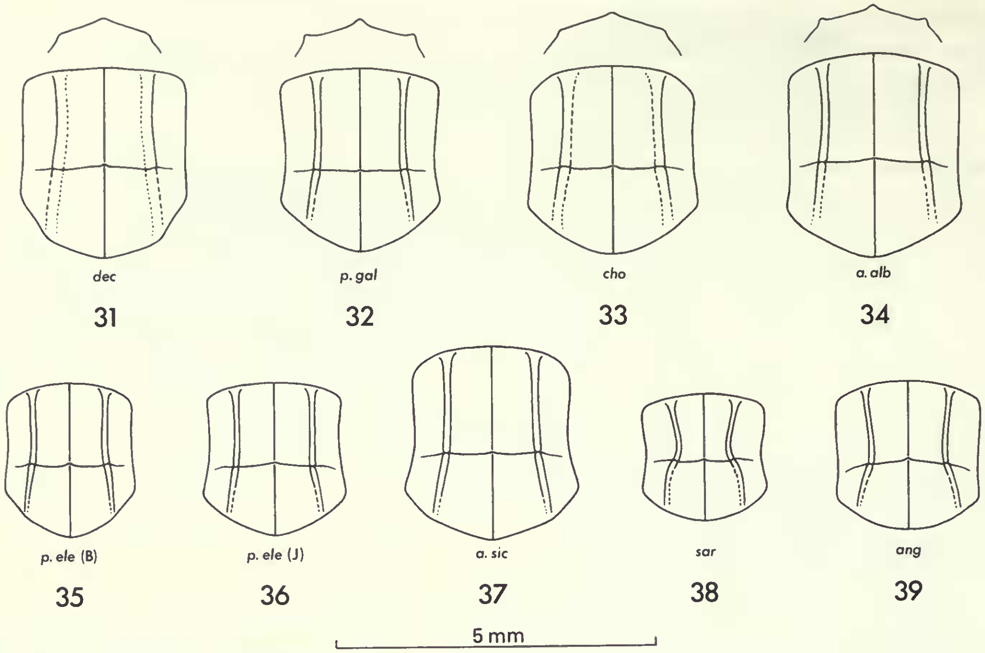
– Known only from North Africa and the Balearic Islands. Pronotal lateral carinae relatively high and narrow, as in Fig. 34. Coloration more uniform 5

5 Known only from North Africa. Larger: length of hind femur usually more than 9·4 mm in ♂, more than 12·6 mm in ♀; length of pronotum usually more than 2·7 mm in ♂; length of fore wing usually less than 1·22 times length of hind femur in ♀ **E. albolineatus albolineatus** (Lucas) (p. 135)

– Known only from the Balearic Islands. Smaller: length of hind femur usually less than 9.4 mm in



Figs 25–30 Side view of typical specimens of each sex of (25, 26) *Euchorthippus declivus*, (27, 28) *E. pulvinatus gallicus* and (29, 30) *E. chopardi*.



Figs 31–39 Dorsal view of the pronotum of (31) *Euchorthippus declivus*, (32) *E. pulvinatus gallicus*, (33) *E. chopardi*, (34) *E. albolineatus albolineatus*, (35) *E. pulvinatus elegantulus* from Brittany, (36) *E. p. elegantulus* from Jersey, (37) *E. albolineatus siculus*, (38) *E. sardous*, (39) *E. angustulus*. Diagrammatic profiles of cross-sections of the pronotal disc are also shown in Figs 31–34.

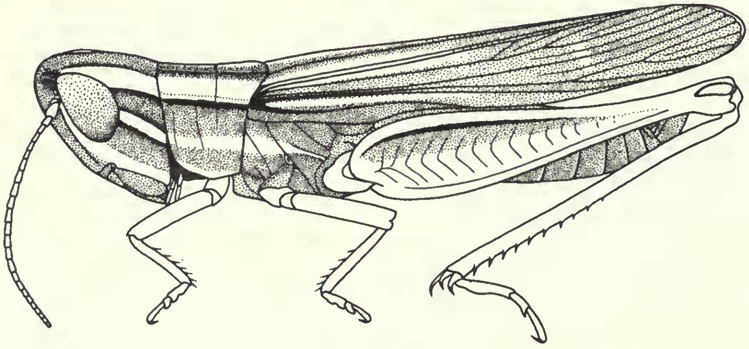


Fig. 40 Dorsolateral view of a typical male of *Euchorthippus chopardi*, showing the characteristic colour pattern.

♂, less than 12·6 in ♀; length of pronotum usually less than 2·7 mm in ♂; length of fore wing usually more than 1·22 times length of hind femur in ♀ .... ***E. angustulus*** Ramme (p. 137)

6 Known only from Sicily. Stridulatory file with fewer than 110 pegs in ♂, fewer than 105 pegs or hairs in ♀ .... ***E. albolineatus siculus*** Ramme (p. 136)

– Not known from Sicily. Stridulatory file with more than 115 pegs in ♂, more than 110 pegs or hairs in ♀ 7

7 Larger: length of head usually more than 2·4 mm in ♂, more than 3·2 mm in ♀; length of fore wing usually more than 9·2 mm in ♂, more than 11·3 mm in ♀. (Southern half of France, Iberian Peninsula) .... ***E. pulvinatus gallicus*** Mařan (p. 131)

– Smaller: length of head usually less than 2·4 mm in ♂, less than 3·2 mm in ♀; length of fore wing usually less than 9·2 mm in ♂, less than 11·3 mm in ♀. (Jersey and southern Brittany) .... ***E. pulvinatus elegantulus*** Zeuner (p. 131)

Descriptions of the species

Euchorthippus declivus (Brisout)

(Figs 25, 26, 31)

Acridium declivum Brisout, [1849]: 420. LECTOTYPE ♀, FRANCE: near Paris, St-Germain (MNHN, Paris), here designated [examined].

Stenobothrus pulvinatus var. *gracilis* Azam, 1901: 46. LECTOTYPE ♂, FRANCE: near Clermont-Ferrand, Puy de Crouelle, viii.1896 (*M. H. du Buysson*) (MNHN, Paris), here designated [examined]. [Synonymized by Chopard, 1952: 303.]

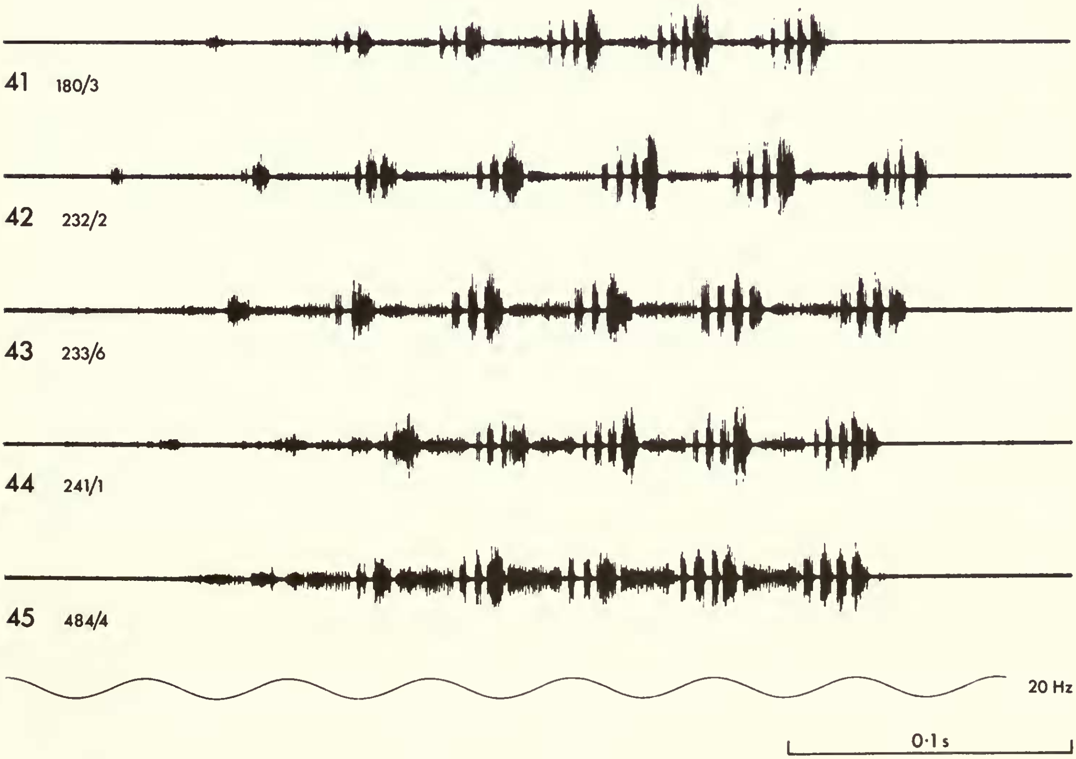
Euchorthippus declivus (Brisout) Uvarov, 1926: 341.

Euchorthippus declivus meridionalis Jannone, 1937: 57. LECTOTYPE ♂, ITALY: Puglia, Monte Angeli, 2.ix.1935 (IEA, Portici), here designated [examined]. [Synonymized by La Greca, 1959: 138.]

Euchorthippus declivus štíchai Mařan, 1954: 137. Holotype ♂, CZECHOSLOVAKIA: Kamemín, viii.1952 (*J. Mařan*) (NM, Prague) [examined]. [Synonymized by Harz, 1975: 924.]

DIAGNOSIS. ♂♀. Pronotal lateral carinae relatively low and broad; length of pronotum usually 0·98–1·41 times length of head. Fore wings relatively short, not or hardly reaching apical quarter of hind femora in ♂, middle of hind femora in ♀, but usually projecting beyond hind wings by at least 0·8 mm in ♂, at least 0·5 mm in ♀; distance from stigma to tip of fore wing usually less than 0·21 times length of hind femur in ♂, less than 0·25 in ♀. Length of hind wing usually less than 0·87 times length of hind femur in ♂, less than 0·78 in ♀. Male stridulatory file usually with 75–120 pegs. Male subgenital plate relatively long and pointed, as in Fig. 25. (Full data for measurements, ratios and number of stridulatory pegs are given in the bar-charts on pp. 144–150.)

Male calling song (see Figs 14, 17, 41–45). Each echeme usually with 10–15 gaps. Other song characters as shown in bar-charts (p. 119).



Figs 41–45 Oscillograms of single echemes from the calling songs of five French males of *Euchorthippus declivus*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 107, 108).

DISCUSSION. This is the most easily recognizable of the mainland species of *Euchorthippus* in western Europe. As can be seen in Figs 8, 84 and 88, the projection of the fore wings beyond the hind wings (when both pairs of wings are flexed) enables the males, and usually the females, to be identified at once. In all the other western Palaearctic species (except *madeirae* – see below) the tips of the two pairs of flexed wings are coincident or almost so in live or freshly killed specimens, though a very small gap often develops in dried specimens. The length of the hind wing and the distance from the stigma to the tip of the fore wing, both taken as a ratio with the length of the hind femur, also provide good characters in both sexes (see Figs 10, 11, 84, 85, 87, 88). The male is further characterized by the relatively long and pointed subgenital plate (Fig. 25).

The endemic Madeiran species *E. madeirae* Uvarov resembles *declivus* in having rather low, broad pronotal lateral carinae and short wings, with the fore wings extending well beyond the hind wings. However, the males have a much shorter and blunter subgenital plate than *declivus*, and the pronotal lateral carinae are more clearly incurved in both sexes.

There is a rare macropterous form of *declivus* in which the fore wings reach a length of 11–13 mm in the male and 13–15 mm in the female. This form has been recorded from the south-western Slovakian steppe in Czechoslovakia by Mařan (1957: 189) and from Gran Sasso, Abruzzi, Italy by Baccetti (1958: 426–428); we have seen further specimens from Rome and from near Banja Luka in Yugoslavia. In the specimens we have examined the fore wings project beyond the hind wings by much less than is typical of *declivus* and the distance from the stigma to the tip of the fore wing is usually larger, but they can be distinguished from *pulvinatus* by the relatively low pronotal lateral carinae and, in the male, the shape of the subgenital plate. Dr J. J. Presa has kindly informed us that he now believes that his records of this form from the Sierra de Guadarrama, Spain (Presa, 1978: 125) were based on misidentified *pulvinatus*.

The calling song of the male (see Figs 14, 41–45) cannot be recognized as *declivus* with the unaided ear, but oscillographic analysis shows that it has a larger number of gaps per echeme than both *pulvinatus* and *chopardi* (see p. 119 for further discussion).

In France *declivus* occurs further north than *pulvinatus* and *chopardi* and seems, as one would expect, to be more hygrophilous. It probably shows a similar ecological preference in northern Spain, but in Italy, where it is apparently the only species of *Euchorthippus* to occur on the mainland, it seems to be able to tolerate drier conditions, tending to occupy the habitats associated with all three species in France and Spain.

For discussion of the transfer of the subspecies *elegantulus* from *declivus* to *pulvinatus* see p. 131.

We have examined seven female specimens, three from the MNHN, Paris and four from the IRSNB, Brussels, that have been regarded in these institutions as syntypes of *Acridium declivum* Brisout. We have also examined a number of further specimens of both sexes from the IRSNB that had previously been in the collection of de Selys Longchamps (who had earlier acquired Brisout's collection) and that could therefore also be regarded as possible syntypes of this species. Of all these specimens only one is labelled as being from one of the four type-localities named by Brisout (1849: 420); this is one of the three female specimens from the MNHN and is labelled 'St Germain'. We feel that this is the only specimen we have examined that can be regarded with confidence as a syntype and we have accordingly selected and labelled it as lectotype.

We have examined the male and female syntypes of *Stenobothrus pulvinatus* var. *gracilis* Azam, and have selected and labelled the male as lectotype.

We have also selected and labelled a male lectotype from the type-series of *Euchorthippus declivus meridionalis* Jannone. This specimen, from Monte Angeli, is in much better condition than the male specimen labelled 'Tipo' by Jannone, which was from Altamura.

MATERIAL EXAMINED

Primary types (see synonymy) and 558 other specimens from the following localities.

France. Marne (no further data). Paris. Yvelines: St-Germain. Essonne: Lardy. Seine-et-Marne: Fontainebleau; Fontainebleau Forest; Episy. Haute-Marne: Colombey-les-Deux-Eglises. Loire-

Atlantique: Varades. Yonne: 33 km E. of Sens, near Villeneuve-l'Archevèque. Cher: 23 km S. of Briare. Nièvre: La Charité. Puy-de-Dôme: 12 km N. of Thiers; near Besse-en-Chandesse, Saurier; near Clermont-Ferrand, Puy de Crouelle; near Issoire, Clémensat. Dordogne: Bergerac; near Le Bugue, Campagne. Savoie: Flumet. Haute-Loire: St-Paulien; 5 km N. of Le Puy; 16 km S. of Cascades de la Baume. Lot: near Souillac. Ardèche: near Privas. Lozère: 34 km N. of Mende; near Mende, Col de Montmirat. Drôme: near Valdrôme. Landes: near Arcachon, Biscarrosse; near Morcenx. Vaucluse: Mont Ventoux; near Carpentras, Bédoin. Alpes-de-Haute-Provence: N. of Digne, La Rouine, 760–1070 m. Hérault: 5 km E. of Montpellier. Haute-Garonne: 15 km N. of Toulouse. Alpes-Maritimes: near St-Dalmas-de-Tende; Col de Vence, 930 m; near Grasse, Gréolières; Mt Courmette; Thorenc; St-Martin-Vésubie; Auron, 1580 m. Var: *c.* 4 km W. of Cannes, Esveral; near Comps-sur-Artuby, Bargème. Pyrénées-Orientales: Vernet-les-Bains, near Le Perthus.

Spain. Santander: Playa de Cóbreces. León: Riaño. Huesca: Ordesa. Teruel: Montoro de Mezquita, Masada del Cerro, 1300 m; Villarluengo, 1270 m.

Italy. Piemonte: Voltaggio. Liguria: Chiavari; Portofino, Vetta; near Sestri, Bracco Pass, 600 m. Emilia Romagna: Vetto. Toscana: near M. Amiata, 4 km SW. of Bagni San Fillipo; 17 km E. of Siena; Siena, near Colleverde camp site; near Firenze, Futa Pass. Abruzzi: Gran Sasso d'Italia, Fonte Cerreto, near Staz Funivia, 340 m; G.S.I., 2 km SW. of Valle Fredda; Civitella del Tronto. Lazio: Roma; near Casa del Corta; between Acquapendente and Lake Bolzena. Puglia: Monte Angeli; Altamura. Basilicata: Venosa, 420 m; Varco di Pietrastretta, near Potenza, 850 m.

DISTRIBUTION (see Fig. 81). All France except for the north-western peninsulas and the extreme north and north-east; northern and north-eastern Spain; southern Switzerland; most of Italy; Sicily and Sardinia. Central and eastern Europe (as far north as southern and eastern Austria, southern Czechoslovakia and south-western Ukraine); most of the Balkan Peninsula; Asia Minor. *E. declivus* seems to be the only species of *Euchorthippus* occurring in mainland Italy, where it is widespread.

There have been a number of published records of *declivus* from various parts of Spain; the more recent ones include those of Gangwere & Morales (1970: 58), Presa (1978: 125), Herrera (1979: 59), González (1981: 61), Presa & García (1982: 130) and Defaut (1982: 82, 85). In his recent catalogue Herrera (1982: 105) lists for *declivus* eight widely scattered Spanish provinces. Following an examination of specimens kindly lent to us by Drs L. Herrera and M. J. González, we consider their records for the provinces of Navarra and Salamanca, respectively, to be based in misidentified *pulvinatus*, and Dr J. J. Presa has informed us that he now believes the same to apply to his records from the Sierra de Guadarrama and the record from Murcia province cited in his joint paper with Dr M. D. García. Dr B. Defaut has kindly lent us the specimens on which his record from Teruel province was based and we agree with his identification. We have not been able to check the basis for the remaining records but, in view of the frequent confusion between these two species in Spain, are inclined to regard all Spanish records of *declivus* as needing confirmation. Apart from those mentioned above from Teruel province, the only Spanish specimens of *declivus* we have seen were from Santander, León and Huesca provinces and were kindly lent to us by Dr G. Kruseman of the Instituut voor Taxonomische Zoölogie, Amsterdam, Dr V. Llorente of the Instituto Español de Entomología, Madrid, and Dr J. L. Santos of the Universidad Complutense, Madrid. The 97 specimens of *Euchorthippus* from the Iberian Peninsula in the BMNH are all either *pulvinatus* or *chopardi*, and we have not seen *declivus* during our own visits to Spain.

Euchorthippus pulvinatus (Fischer de Waldheim)

(Figs 27, 28, 32, 35, 36)

Oedipoda pulvinata Fischer de Waldheim, 1846: 305. Type-material lost. Type-localities, U.S.S.R.: near Moscow; Kazan? ('Casan'); Karabag? ('Karabagh'); Caucasus.
Euchorthippus pulvinatus (Fischer de Waldheim) Tarbinskii, 1926: 192.

The nominate subspecies of *pulvinatus* does not occur in western Europe and has thus been excluded from this study. We have considered it best not to take it into account in the diagnosis given below, which is therefore based only on the two western subspecies *gallicus* and *elegantulus*. Most of the characters given in the diagnosis are probably equally true of *p. pulvinatus*, but this subspecies has longer wings, the fore wings usually reaching the tips of the hind femora in both sexes. The brief diagnoses given for *gallicus* and *elegantulus* include only the characters by which these two subspecies differ from each other.

DIAGNOSIS. ♂♀. Pronotal lateral carinae relatively high and narrow; length of pronotum usually 0·88–1·20 times length of head in ♂, 0·97–1·32 in ♀. Fore wings not usually reaching tips of hind femora in ♂, not reaching bases of genicular lobes in ♀; distance from stigma to tip of fore wing usually 0·20–0·33 times length of hind femur in ♂, 0·26–0·37 in ♀. Length of hind wing usually 0·91–1·16 times length of hind femur in ♂, 0·79–1·00 in ♀. Stridulatory file usually with 115–165 pegs in ♂, 115–145 pegs or hairs in ♀. Male subgenital plate of moderate length and tending to be slightly pointed, as in Fig. 27. (Full data for measurements, ratios and number of stridulatory pegs are given in the bar-charts on pp. 144–150.)

Male calling song (see Figs 15, 18, 46–64, 66–70). Echeme repetition rate usually 0·8–1·6/s. Syllables usually lasting 20–35 ms. Other song characters as shown in bar-charts (p. 119).

DISCUSSION. This species can be easily distinguished from *declivus* by the characters listed and discussed under that species. Distinguishing *pulvinatus* from *chopardi* where their ranges overlap in southern France and the Iberian Peninsula is much more difficult, especially if a reliable reference collection is not available. *E. pulvinatus* almost always lacks the strong longitudinally striped colour pattern typical of *chopardi* (Fig. 40). The shorter fore wings (Figs 27, 28, 83, 87) and prominent, narrow pronotal lateral carinae (Fig. 32) provide good morphological characters, and the distance from the stigma to the tip of the fore wing, taken as a ratio with the length of the hind femur, is usually much smaller than in *chopardi* (Figs 85, 88).

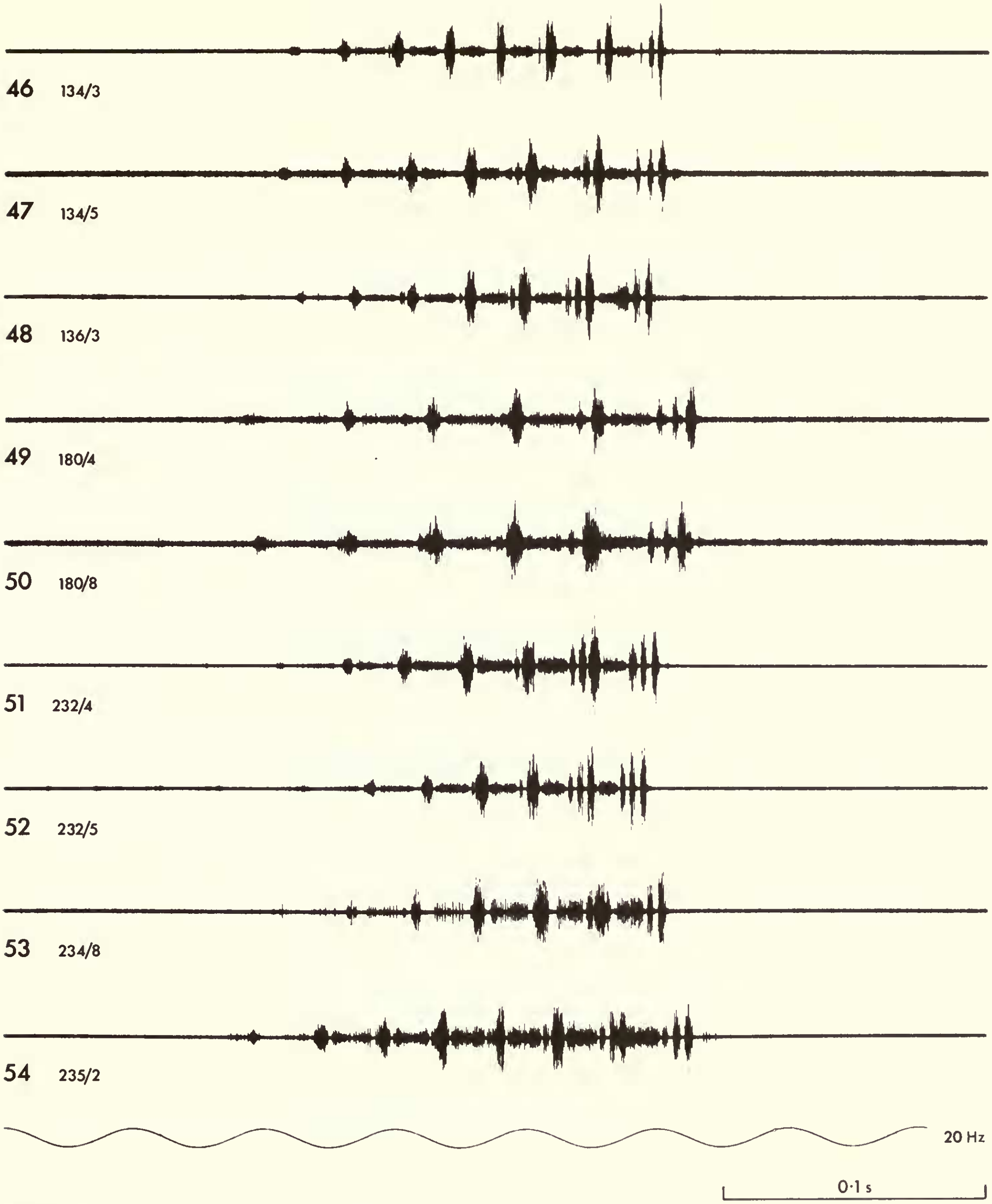
The best numerical method we have found for separating males of these two species is by combining the number of stridulatory pegs, the distance from the stigma to the tip of the fore wing and the ratio of the length of the pronotum to the length of the head, and plotting the result on a triangular graph (Fig. 12; see p. 110 for a full explanation). A simpler but rather less effective separation can be obtained by plotting two of these characters, stridulatory pegs and stigma distance, on a two-axis graph (Fig. 9); this gives a particularly good separation for French specimens. Both sexes can be separated quite well by plotting stigma distance against length of hind femur, as shown in Figs 10, 11; there is no overlap within our French and Iberian samples, but in the male there is a slight overlap between our samples of Iberian *pulvinatus* and French *chopardi*.

Because of the variable effect of shrinkage during drying, we have not found either the shape or the dimensions of the male subgenital plate to be particularly useful in distinguishing between dried specimens of *pulvinatus* and *chopardi* (see Fig. 85 for a comparison of the dimensions).

The male calling song of *pulvinatus* can usually be distinguished from that of *chopardi* by the faster echeme repetition rate, as shown in Figs 15, 16. Oscillographic analysis shows that the duration of the echemes, and especially of the syllables, is shorter than that of *declivus* and *chopardi* (Figs 18–20).

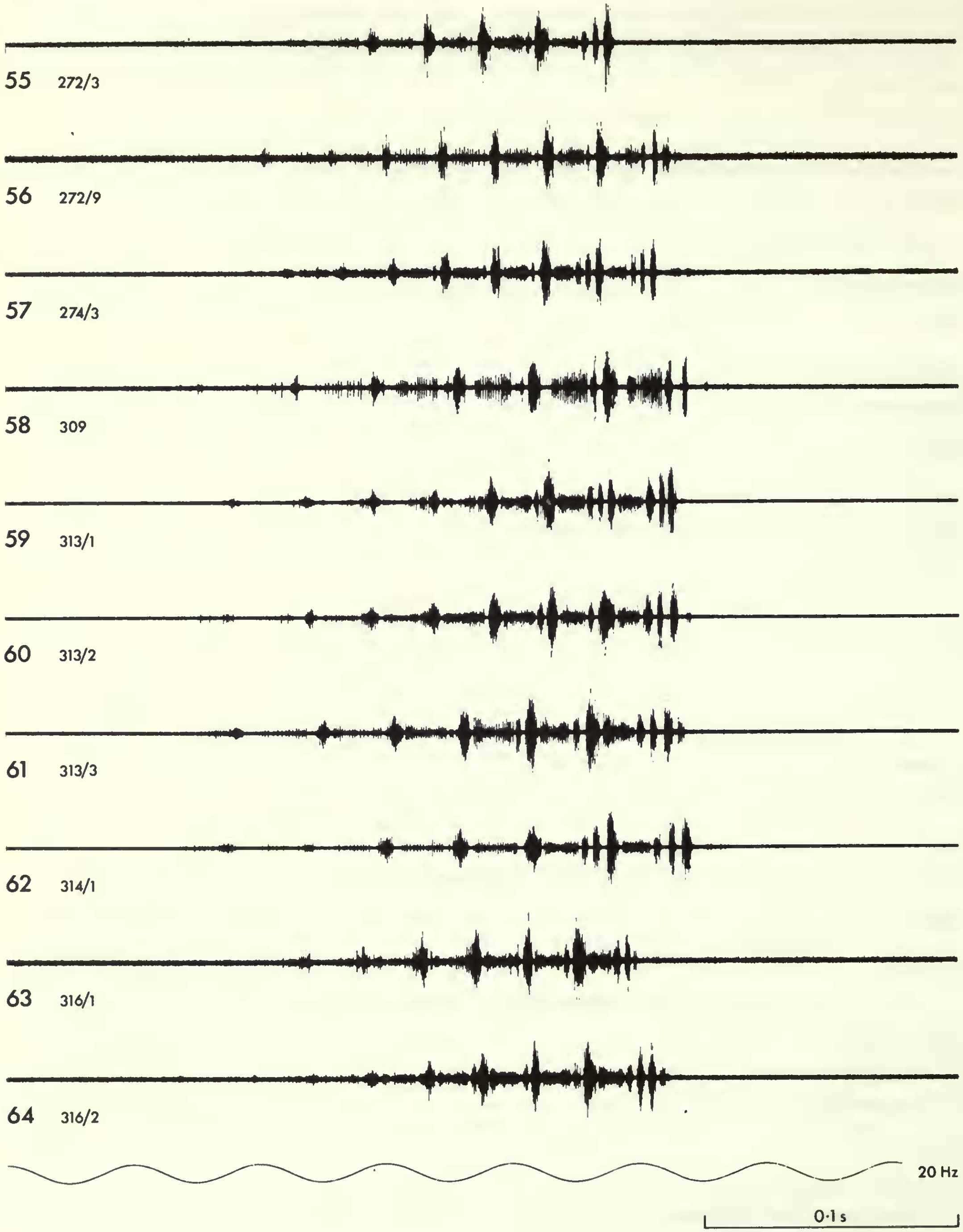
In France the range of *pulvinatus* extends much further north than that of *chopardi* and Descamps (1968) has suggested that the former is less xerophilous than the latter (while being more so than *declivus*). There is, however, some indication from the material we have examined that this may not be so in Spain. Nearly all the specimens we have seen from the extreme south of Spain have been *pulvinatus* and, although Pascual (1978) has shown that *chopardi* occurs in the Sierra Nevada, he found it only at altitudes of 1800–2000 m, whereas *pulvinatus* occurred at the lower altitudes of 1250–1450 m.

DISTRIBUTION (see Fig. 81). In western Europe this species occurs in Jersey, France and the Iberian Peninsula. The eastern subspecies, *p. pulvinatus*, occurs as far west as Czechoslovakia (Čejchan, 1981; 1982), eastern Austria and the Balkan Peninsula, and extends eastwards through the Ukraine, southern Russia, Asia Minor, Kazakhstan and Central Asia to China. The range of this species thus appears to be divided into two by quite a large gap, approximately between longitudes 7°E and 13°E and including Switzerland, western Austria and the whole of Italy; there have been some references in the literature to the occurrence of *pulvinatus* in Italy



Figs 46–54 Oscillograms of single echemes from the calling songs of nine French males of *Euchorthippus pulvinatus gallicus*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 107, 108).

(e.g. La Greca, 1959: 139), but we have seen no Italian specimens of *pulvinatus* ourselves and are at present unconvinced by such references. If this gap is indeed a real one, it would clearly account for the morphological divergence between *p. gallicus* and the nominate subspecies (see also p. 140).



Figs 55–64 Oscillograms of single echemes from the calling songs of ten Spanish males of *Euchorthippus pulvinatus gallicus*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 107, 108).

Euchorthippus pulvinatus gallicus Mařan

(Figs 27, 28, 32)

Euchorthippus pulvinatus gallicus Mařan, 1957: 187. Holotype ♂, FRANCE: Draguignan, 1898 (*N. Kheil*) (NM, Prague) [examined].

DIAGNOSIS. ♂♀. Length of head usually more than 2·4 mm in ♂, more than 3·2 mm in ♀. Length of fore wing usually more than 9·2 mm in ♂, more than 11·3 mm in ♀. Length of hind femur usually more than 8·4 mm in ♂, more than 11·8 mm in ♀. (See also bar-charts on pp. 144–150.)

DISCUSSION. For the best methods of distinguishing *p. gallicus* from the closely similar species *chopardi*, see the species 'Discussion' for *pulvinatus* (p. 128). The relationship between this subspecies and *p. elegantulus* is discussed under that subspecies.

MATERIAL EXAMINED

Holotype (see above) and 573 other specimens from the following localities.

France. Charente-Maritime: Saintes. Haute-Vienne: Limoges. Puy-de-Dôme: near Clermont-Ferrand. Dordogne: near Le Bugue, Campagne; Bergerac. Lot: near Souillac. Lot-et-Garonne: near Agen. Ardèche: near Privas. Drôme: near Nyons, 600 m; near Valdrôme. Hautes-Alpes: near Laragne-Montéglin, Saléon. Aveyron: near Millau. Landes: Arcachon; near Morcenx. Gard: between Arles and Nîmes. Vaucluse: near Carpentras, Bédoin; Mont Ventoux, near Les Bruns; 3 km SE. of Cavaillon. Hérault: several localities near Montpellier. Haute-Garonne: 15 km N. of Toulouse. Alpes-Maritimes: near Villefranche-sur-Mer; Cap d'Ail; Biot; Le Rouret; Sarrée Valley, 600 m; near Nice, Cagnes. Bouches-du-Rhône: near Cassis; Petit Camargue, 22 km SE. of Arles, near Mas Thiberte; P.C., Stes-Maries-de-la-Mer; 14 km E. of Salon. Var: Draguignan; Bagnoles; Montouroux; near Toulon, La Seyne-sur-Mer; Hyères; La St-Baume. Pyrénées-Orientales: near Banyuls-sur-Mer; near St-Cyprien Plage; St-Cyprien; Vernet-les-Bains; near Le Perthus.

Spain. Vizcaya: Sopelana. Burgos: 2 km S. of Lerma. Huesca: 1 km SE. of Seo de Urgel; near Ortedo, 7 km SE. of Seo de Urgel; 2 km SE. of Ainsa; 5 km NW. of Solsona. Gerona: Port Bou; near Vilajuiga. Zaragoza: 12 km E. of Caspe. Salamanca: 5 km N. of Castraz, Rio Yaltes; Cervera; Cristo de La Laguna; Rodillo. Madrid: Sierra de Guadarrama; Madrid. Guadalajara: near Pastrana. Teruel: Albarracin. Cuenca: Belmonte; near Uña. Valencia: Requena, 700 m. Jaén: Sierra de Cazorla, W. of Nava del Espino, 1600–1700 m; S.C., Nava de S. Pedro, 1400 m; S.C., Puente de Las Harrerias. Murcia: Moratalla. Huelva: near Ayamonte. Málaga: near Torremolinos, Roya Miel.

Portugal. Guarda: Guarda. Leiria: Serra do Condieiros, near Alcanena, Ribatejo; Caldas da Rainha. Lisboa: Mafra; Ericeira; Lisboa, Parque Florestal de Monsanto. Evora: Evora. Setúbal: R. Sado, near Marateca.

DISTRIBUTION (see Fig. 81). Central and southern France; Iberian Peninsula. The specimens on which Ebner (1931: 501) based his record of *pulvinatus* from Majorca have been lost and we consider the occurrence of this species in the Balearic Islands to be doubtful.

Euchorthippus pulvinatus elegantulus Zeuner

(Figs 35, 36)

Euchorthippus elegantulus Zeuner, 1940: 107. Holotype ♂, JERSEY: Ouainé Bay, 4.ix.1938 (*F. E. Zeuner*) (BMNH, London) [examined].

Euchorthippus declivus elegantulus Zeuner; Mařan, 1957: 189; Descamps, 1968: 5.

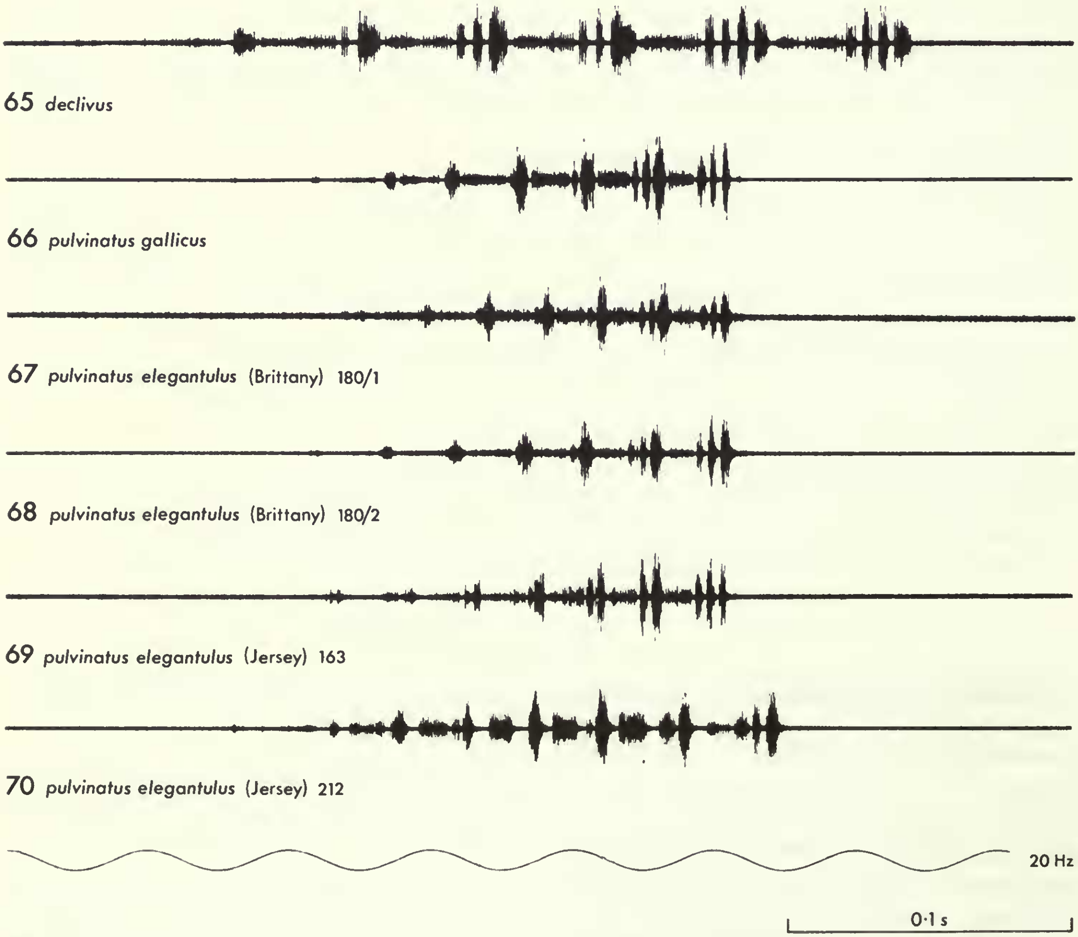
[*Euchorthippus declivus* (Brisout); Harz, 1975: 924. Erroneous synonymy.]

DIAGNOSIS. ♂♀. Length of head usually less than 2·4 mm in ♂, less than 3·2 mm in ♀. Length of fore wing usually less than 9·2 mm in ♂, less than 11·3 mm in ♀. Length of hind femur usually less than 8·4 mm in ♂, less than 11·8 mm in ♀. (See also bar-charts on pp. 144–150.)

DISCUSSION. This subspecies is essentially a small form of *pulvinatus*, the head showing the size difference most clearly (see Figs 82, 86).

One of the more interesting conclusions to emerge from this study has been the fact that *elegantulus*, which has hitherto always been associated with *declivus*, is much closer to *pulvinatus* in both morphological characters and song. When Zeuner (1940) originally described *elegantulus* (as a full species) he stated that it was related to *declivus* and compared the two in several characters while making no mention of *pulvinatus*. Chopard (1952) suggested that it 'n'est sans doute qu'une sous-espèce de *declivus*' and, probably following this lead, Mařan (1957) and Descamps (1968) treated it formally as a subspecies of *declivus*. Harz (1975) went even further, regarding it as no more than a synonym of *declivus*.

This association of *elegantulus* with *declivus* probably stemmed from the fact that the subgenital plate of the Jersey males is usually more pointed than is typical of *pulvinatus* and is sometimes nearer in shape to *declivus*. However, in all other morphological characters *elegantulus* is closer to *pulvinatus* than to *declivus*, and in some characters resembles *pulvinatus* very closely; this is well shown by the bar-charts of the projection of fore wing beyond hind wing (Figs 84, 88), by those of ratios (Figs 81, 83–87), in which the effect of size is largely eliminated, and by all the scatter diagrams, including the triangular graph (Figs 8–13). Zeuner (1940) even included in his description of *elegantulus* the fact that the median and lateral carinae of the pronotum are 'very pronounced for the genus', another character shared with *pulvinatus* but not with *declivus*. The close relationship with *pulvinatus* is confirmed by the song of *elegantulus*, which agrees closely with that of *pulvinatus gallicus* in all respects, while showing a marked contrast with *declivus* in the number of gaps per echeme and the duration of both the echemes and the syllables (Figs 20–24, 65–70).



65 *declivus*

66 *pulvinatus gallicus*

67 *pulvinatus elegantulus* (Brittany) 180/1

68 *pulvinatus elegantulus* (Brittany) 180/2

69 *pulvinatus elegantulus* (Jersey) 163

70 *pulvinatus elegantulus* (Jersey) 212

Figs 65–70 Oscillograms of single echemes from the calling songs of four males of *Euchorthippus pulvinatus elegantulus*, with typical echemes from the male calling songs of *E. declivus* and *E. pulvinatus gallicus* added for comparison. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 108).

A further point of interest resulting from this study is that a form closely resembling the Jersey population of *elegantulus* occurs in the southern part of Brittany, in the region extending from Quiberon to Le Croisic. The Breton specimens are, on average, not quite as small as specimens from Jersey, and the male subgenital plate is usually blunter, more like typical *pulvinatus*. However, the bar-charts of absolute measurements (Figs 82–88) show that the Breton population is generally much closer to Jersey *elegantulus* than to French *gallicus*, and we think it reasonable, at least for the time being, to recognize these two populations as together constituting the subspecies *elegantulus*. When the distribution and ecology of these forms have been more thoroughly studied, it may prove to be more sensible to regard the Jersey and Brittany populations as representing no more than island and coastal forms of *gallicus*, living under rather unfavourable conditions at the northern limit of the climatic tolerance of this subspecies. A statistical comparison between our samples of *gallicus* and *elegantulus* gives t values of 9·5 for head length, 8·8 for fore wing length and 9·0 for hind femur length in the male, and corresponding values of 7·7, 7·3 and 6·7 in the female. The table given by Géry (1962) shows that all these values indicate a non-overlap between these samples of between 75 per cent and 90 per cent, which does not lend very strong support to their recognition as separate subspecies.

MATERIAL EXAMINED

Holotype (see p. 131) and 39 other specimens from the following localities.

Jersey. Quennevais; Blanches Banques; St Ouen's Pond; Ouainé Bay; St Helier.

France. Morbihan: Quiberon; Malanzac. Loire-Atlantique: 3 km SW. of Guérande; near Guérande, Le Croisic.

DISTRIBUTION (see Fig. 81). Known only from Jersey and the extreme south of Brittany. In addition to the four Breton localities listed above, the record of *pulvinatus* from 'landes de Plescop, environs de Vannes' given by Sellier (1947) almost certainly refers to this subspecies.

Euchorthippus chopardi Descamps

(Figs 29, 30, 33, 40)

Euchorthippus chopardi Descamps, 1968: 8. Holotype ♂, FRANCE: Vaucluse, Cavaillon, route forestière du Luberon, 150 m (*M. Descamps*) (MNHN, Paris) [examined].

DIAGNOSIS. ♂♀. Head and pronotum usually with conspicuous dark and light longitudinal stripes (Fig. 40). Pronotal lateral carinae relatively low and broad, almost straight and parallel in metazona; length of pronotum usually 0·85–1·25 times length of head. Fore wings relatively long, usually reaching at least tips of hind femora in ♂, bases of genicular lobes in ♀; distance from stigma to tip of fore wing usually 0·33–0·46 times length of hind femur in ♂, 0·40–0·54 in ♀. Length of hind wing usually 0·98–1·32 times length of hind femur in ♂, 1·01–1·29 in ♀. Male stridulatory file usually with 95–160 pegs. Male subgenital plate relatively short and blunt, as in Fig. 29. (Full data for measurements, ratios and number of stridulatory pegs are given in the bar-charts on pp. 144–150.)

Male calling song (see Figs 16, 19, 71–77). Echeme repetition rate usually 0·5–0·7/s. Other song characters as shown in bar-charts (p. 119).

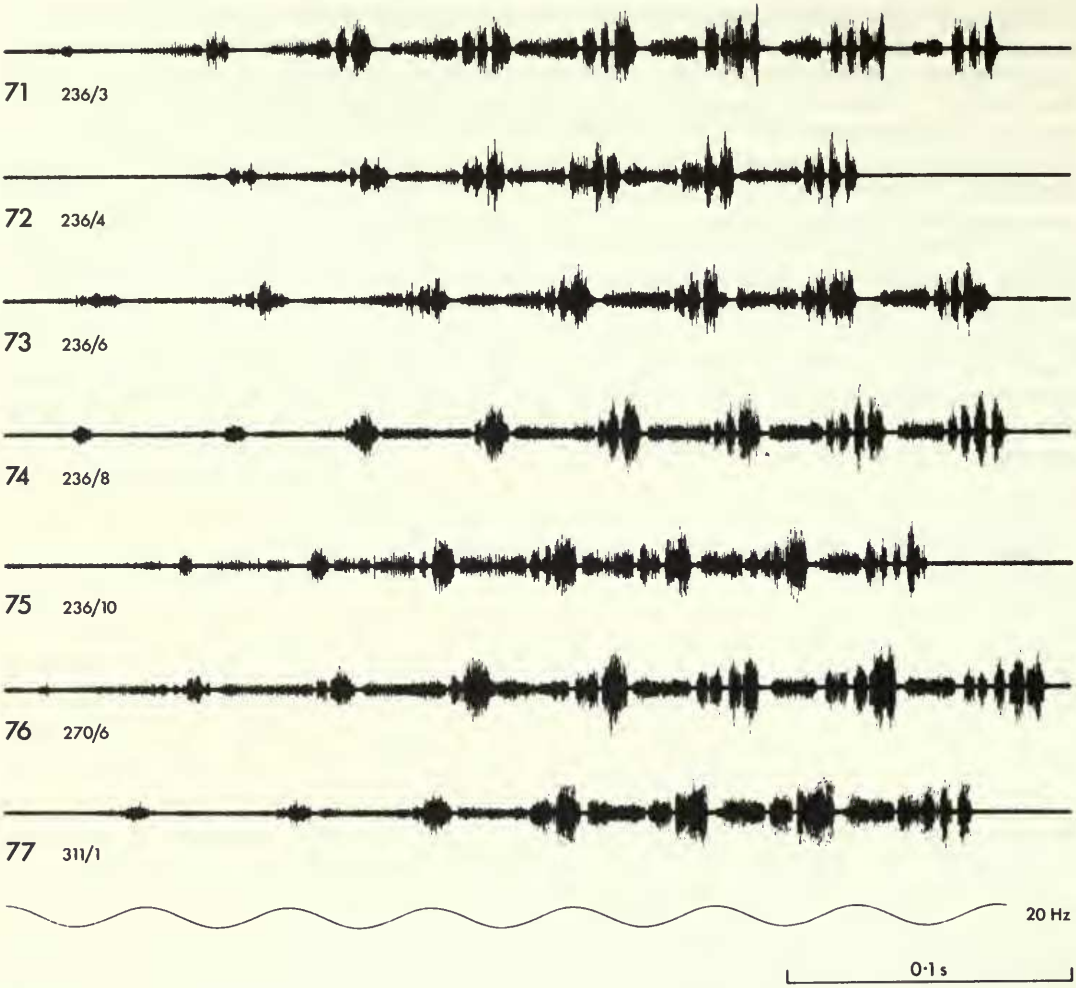
DISCUSSION. For the easy separation of this species from *declivus* see the 'Discussion' under that species. The much more difficult separation of *chopardi* from *pulvinatus* is discussed fully under the latter species. The usual longitudinally striped colour pattern of *chopardi* (Fig. 40) provides a strong indication of its identity, and this can be confirmed for males by plotting their relevant measurements and peg-counts on the triangular graph shown in Fig. 12, and for either of the sexes by plotting their measurements on the scatter diagrams shown in Figs 9–11. For the best means of distinguishing *chopardi* from *albolineatus* see the 'Discussion' under that species.

MATERIAL EXAMINED

Holotype (see above) and 122 other specimens from the following localities.

France. Vaucluse: 3 km SE. of Cavaillon (type-locality); Mont Ventoux, 600–1200 m; near Carpentras, 3 km S. of Malaucène. Hérault: 5 km E. of Montpellier. Pyrénées-Orientales: Banyuls-sur-Mer; Vernet-les-Bains; near Vernet-les-Bains, Corneilla-de-Conflent.

Spain. Orense: Leiro. Huesca: 8 km E. of Ainsa. Gerona: Port Bou. Zaragoza: 3 and 4·5 km E. of



Figs 71–77 Oscillograms of single echemes from the calling songs of five French (71–75) and two Spanish (76, 77) males of *Euchorthippus chopardi*. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 107, 108). Note that recordings 236/3, 236/4 and 236/6 were made at the type-locality.

Caspe. Avila: Sierra de Gredos. Madrid: Sierra de Guadarrama. Cuenca: between Cuenca and Olivares; Belmonte. Valencia: near Gandia; Requena, 700 m. Alicante: near Alicante.

Portugal. Leiria: Serra do Candieiros.

Distribution (see Fig. 81). A species occurring widely in the Iberian Peninsula and extending its range north-eastwards into the French departments bordering the Mediterranean Sea, and Vaucluse. The only published record from the extreme south of Spain is from the Sierra Nevada at altitudes of 1800–2000 m (Pascual, 1978).

Euchorthippus albolineatus (Lucas)

(Figs 34, 37)

Oedipoda albo lineata Lucas, 1849: 38.

In view of the major differences between the Sicilian taxon *siculus* and the North African populations of *albolineatus* (see especially Figs 8–11), we have strong doubts about the current treatment of *siculus* as a subspecies of *albolineatus* (Descamps, 1968; Harz, 1975). We have therefore not attempted to give a diagnosis that includes both these taxa, but have given each of them diagnoses as if they were distinct species. However, as this study is not primarily concerned with either of these taxa, and we have no information on their songs, we prefer to retain the currently used nomenclature for them until their relationships can be more firmly established.

Euchorthippus albolineatus albolineatus (Lucas)

(Fig. 34)

Oedipoda albo lineata Lucas, 1849: 38. LECTOTYPE ♂, ALGERIA: Cercle de Lacalle, Boghar (*H. Lucas*) (MNHN, Paris), here designated [examined].
Euchorthippus albolineatus (Lucas) Uvarov, 1926: 341.
Euchorthippus albolineatus albolineatus (Lucas); Descamps, 1968: 5.

DIAGNOSIS. ♂♀. Pronotal lateral carinae relatively high and narrow; length of pronotum usually 1·00–1·32 times length of head. Fore wings relatively long, usually extending beyond tips of hind femora; distance from stigma to tip of fore wing usually 0·34–0·49 times length of hind femur in ♂, 0·41–0·50 in ♀. Length of hind wing usually 1·10–1·32 times length of hind femur in ♂, 1·04–1·13 in ♀. Male stridulatory file usually 3·28–4·70 mm long, with 100–140 pegs. Male subgenital plate relatively short and blunt (similar to Fig. 29). (Full data for measurements, ratios and number of stridulatory pegs are given in the bar-charts on pp. 144–150.)

DISCUSSION. *E. albolineatus* is at present the only species of the genus known from North Africa and so in practice identification presents no problems. We consider it doubtful that this species occurs in the Iberian Peninsula (see 'Distribution' below), but if it did it could be quite easily confused with *pulvinatus* and *chopardi*. As shown by the triangular graph (Fig. 13) and two-axis scatter diagrams (Figs 9–11), *a. albolineatus* and *chopardi* can be distinguished from *pulvinatus* by the same combination of characters, but in all these diagrams *a. albolineatus* and *chopardi* overlap broadly. The best numerical characters for separating the males are the length of the stridulatory file and the ratio of pronotum to head (see Figs 82, 81), but this ratio is less effective in separating the females. In qualitative characters both sexes of *a. albolineatus* usually lack the strongly striped colour pattern typical of *chopardi* and have more prominent and sharply defined lateral carinae on the pronotum (cf. Figs 33, 34).

E. a. albolineatus is clearly a close relative of both *chopardi* and *pulvinatus*, and is particularly close to *chopardi* in almost all its characters. If it does not occur in the Iberian Peninsula the question arises as to whether it might be better regarded as only subspecifically distinct from *chopardi*. In the absence of any information on the song we can do no more than suggest this as a possibility to be borne in mind in future studies on the group.

We have selected and labelled a male lectotype from the type-series of 10 males and 9 females of *albolineatus*.

MATERIAL EXAMINED

Lectotype (see synonymy) and 124 other specimens from the following localities.

Morocco. Great Atlas Mts, Mouldirt, 1630 m; Oued Kroumane; Meknes district, Ifrane; 10 and 30 km S. of Fez; 12 km SE. of Azrou.

Algeria. Near Algiers, Kouba; near Blida, Chrea, 1300 m; S. of Constantine, El Gehra; Djuradjura Mts, Bouira; Boghar; Boghari; Hauts Plateaux, Trolarel-Taza, 1100 m; Djelfa; Mascara.

Libya. 30 km SW. of Tripoli, near Bianchi.

DISTRIBUTION (see Fig. 81). North Africa, from western Morocco to Tripolitania. In view of the ease with which this species can be confused with *pulvinatus* and *chopardi*, we consider that the records of *albolineatus* from Portugal (Descamps, 1968: 6), Spain (Presa, 1978: 121; González, 1981: 61; Presa *et al.*, 1983) and Majorca (Kruseman, in Harz, 1975: 929) need confirmation.

Euchorthippus albolineatus siculus Ramme

(Fig. 37)

Euchorthippus pulvinatus siculus Ramme, 1927: 161. LECTOTYPE ♂, SICILY: Fontanamurata, 17.vii.1924 (*W. Ramme & W. Richter*) (MNHU, Berlin), here designated [examined].
Euchorthippus albolineatus siculus Ramme; Descamps, 1968: 5.

DIAGNOSIS. ♂♀. Pronotal lateral carinae relatively high and narrow; length of pronotum usually 1·03–1·16 times length of head in ♂, 1·16–1·24 in ♀. Fore wings usually reaching bases of genicular lobes of hind femora in ♂, but usually failing to do so in ♀; distance from stigma to tip of fore wing usually 0·25–0·35 times length of hind femur in ♂, 0·28–0·34 in ♀. Length of hind wing usually 0·97–1·09 times length of hind femur in ♂, 0·90–0·94 in ♀. Stridulatory file usually with 85–110 pegs in ♂, 60–90 pegs or hairs in ♀. Male subgenital plate of moderate length, sometimes tending to be slightly pointed (usually intermediate between the shapes shown in Figs 27 and 29). (Full data for measurements, ratios and number of stridulatory pegs are given in the bar-charts on pp. 144–150.)

DISCUSSION. The status of *siculus* is discussed above under *albolineatus*.

The only other species of *Euchorthippus* known to occur in Sicily (according to Galvagni, 1956: 352 and other authors) is *declivus*, which can be easily distinguished from *siculus* by the characters discussed on p. 126. To judge from the three male specimens we have examined, this sex of *siculus* can be distinguished from most other species of the genus by plotting the number of stridulatory pegs against the stigma distance, as shown in Fig. 9.

The three female specimens we have examined can be separated from *chopardi* and *a. albolineatus* by the distance from the stigma to the tip of the fore wing, especially when taken as a ratio to the length of the hind femur (Figs 11, 88). The only reliable character we have found for separating females of *siculus* from this sex of *pulvinatus* is the number of vestigial pegs or hairs in the stridulatory file, as indicated in couplet 6 of the key (p. 124).

We have selected and labelled a male lectotype from the type-series of *siculus*.

MATERIAL EXAMINED

Lectotype (see synonymy), 2 ♂, 3 ♀ paralectotypes from Fontanamurata and S. Maria de Gésù in Sicily.

DISTRIBUTION. Known only from Sicily.

Euchorthippus sardous Nadig

(Fig. 38)

Euchortippus [sic] *sardous* Nadig, *in* Nadig & Nadig, 1934: 18; La Greca, 1955: 4 [description of ♀ and discussion of relationships]. Holotype ♂, SARDINIA: Gennargentu, 1900 m, 17.vii.1930 (*A. Nadig*) (Coll. Nadig, Chur, Switzerland) [examined].

DIAGNOSIS. ♂♀. Pronotal lateral carinae relatively high and narrow, distinctly incurved in prozona (Fig. 38); length of pronotum less than 2·1 mm in ♂, less than 3·0 mm in ♀, usually 0·85–1·05 times length of head. Length of hind femur usually 6·1–7·1 mm in ♂, 8·2–10·4 mm in ♀. Fore wings usually reaching bases of genicular lobes of hind femora in ♂, but just failing to do so in ♀; distance from stigma to tip of fore wing usually 0·27–0·33 times length of hind femur in ♂, 0·33–0·42 in ♀. Length of hind wing usually 0·90–1·15 times length of hind femur. Male stridulatory file usually with 85–110 pegs. Male subgenital plate relatively short and blunt (similar to Fig. 29). (Full data for measurements, ratios and number of stridulatory pegs are given in the bar-charts on pp. 144–150.)

DISCUSSION. The small size of this endemic Sardinian species, and especially the short pronotum and hind femur (Figs 82, 86), enable both sexes to be easily distinguished from all other species of *Euchorthippus*. The only other species of the genus recorded from Sardinia is *declivus*, which is equally easy to recognize (see p. 126).

MATERIAL EXAMINED

Holotype (see above) and 30 other specimens from the type-locality.

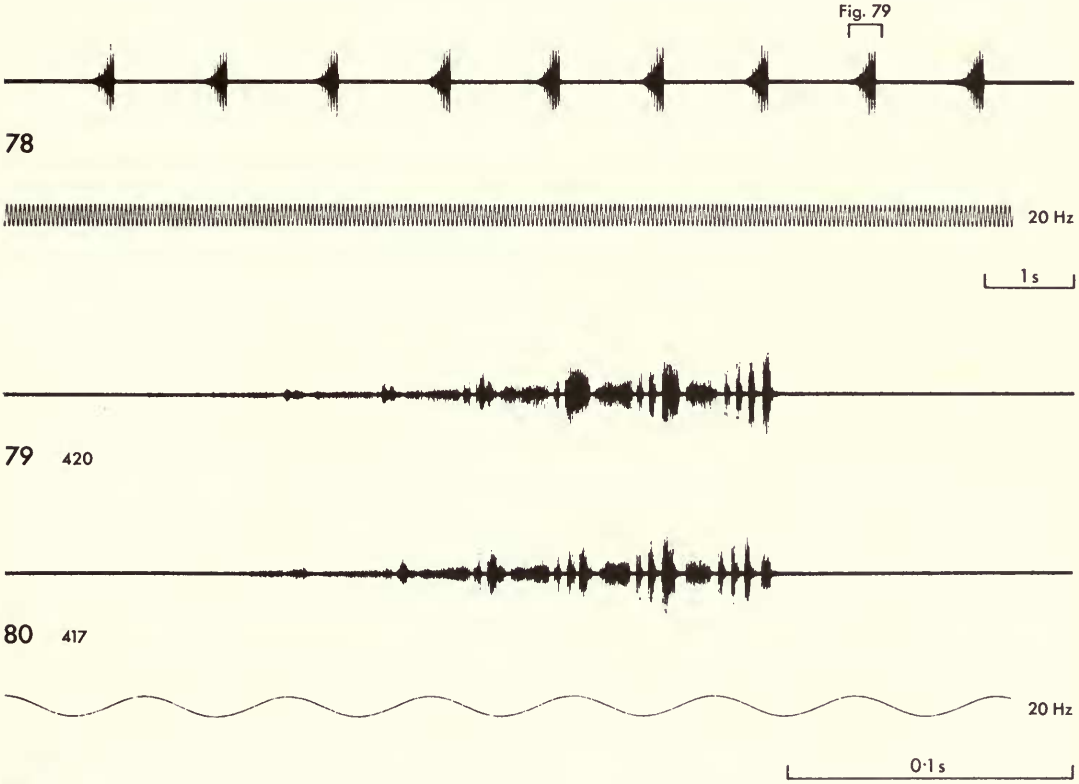
DISTRIBUTION. Known only from the type-locality.

Euchorthippus angustulus Ramme

(Fig. 39)

Euchorthippus angustulus Ramme, 1931: 191. Holotype ♂, Balearic Islands: Formentera, Can Marti, 24–27.vii.1928 (*M. Eisentraut*) (MNHU, Berlin) [examined].

Diagnosis. ♂♀. Pronotal lateral carinae relatively high and narrow. Fore wings usually extending beyond tips of hind femora (usually 1·25–1·40 times length of hind femora); distance from stigma to tip of fore wing usually 0·43–0·56 times length of hind femur in ♂, 0·50–0·61 in ♀. Length of hind wing usually 1·22–1·37 times length of hind femur in ♂, 1·19–1·32 in ♀. Male stridulatory file usually with 103–133 pegs (mean of 25 examined: 119·0±7·70). Male subgenital plate relatively short and blunt (similar to Fig. 29).



Figs 78–80 Oscillograms of the calling songs of two males of *Euchorthippus angustulus*. Fig. 79 is a faster oscillogram of the echeme indicated in Fig. 78. Fig. 80 is taken from the song of another male. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 2 (p. 108).

Male calling song (Figs 78–80). An analysis of songs recorded from two males from Palma Nova, Majorca (not available at the time the bar-charts and scatter diagrams were prepared) gave the following mean values for each male. Echeme repetition rate: 0·84 and 0·85/s. Number of gaps per echeme: 5·6 and 7·4. Duration of echeme: 161 and 164 ms. Duration of syllable: 31 and 32 ms. These figures are based on a total of 179 echemes for the repetition rate and 125 echemes for the other song characters. Comparison with the bar-charts (Fig. 20) shows that the number of gaps per echeme agrees well with *chopardi*, the duration of both the echemes and the syllables is closer to *pulvinatus*, and the echeme repetition rate is intermediate between the two. This confirms Eisentraut's observations, quoted by Ramme (1931: 192), that the song of *angustulus* showed a slower echeme repetition rate than that of *pulvinatus*.

Measurements. The specimens of *angustulus* we have examined were not available at the time the bar-charts were prepared and so their measurements are given separately below (number measured in parentheses; mean followed by standard deviation; all measurements in millimetres). Of the 43 specimens measured, only 5 males and 7 females were available at the time the morphological scatter diagrams were prepared. The measurements of four large females of doubtful identity from northern Majorca are excluded from this list; these specimens are discussed on p. 139.

	Males	Females
Length of head	(26) 2·4–3·0, mean 2·77±0·20	(16) 2·8–3·6, mean 3·21±0·24
Length of pronotum	(25) 2·2–2·8, mean 2·50±0·12	(16) 2·8–3·4, mean 3·16±0·17
Pronotum/head	(25) 0·81–1·06, mean 0·91±0·07	(16) 0·89–1·12, mean 0·99±0·07
Length of hind femur	(25) 7·6–9·2, mean 8·42±0·42	(16) 9·7–11·6, mean 10·51±0·65
Length of stridulatory file	(25) 2·4–3·3, mean 2·88±0·22	
Length of fore wing	(25) 9·7–12·6, mean 11·31±0·61	(16) 12·6–15·6, mean 13·87±0·76
Length of hind wing	(25) 9·4–11·9, mean 10·84±0·55	(16) 12·4–14·3, mean 13·28±0·61
Fore wing/hind femur	(25) 1·27–1·40, mean 1·34±0·04	(16) 1·25–1·40, mean 1·32±0·05
Hind wing/hind femur	(25) 1·22–1·37, mean 1·29±0·04	(16) 1·21–1·32, mean 1·27±0·03
Projection of fore wing beyond hind wing	(25) −0·32–0·24, mean 0·01±0·12	(14) −0·36–0·52, mean 0·10±0·22
Distance from stigma to tip of fore wing	(26) 3·7–4·6, mean 4·16±0·25	(15) 5·6–6·3, mean 6·01±0·20
Stigma distance/hind femur	(25) 0·43–0·56, mean 0·50±0·02	(15) 0·50–0·61, mean 0·56±0·03
Length of subgenital plate	(23) 0·44–0·76, mean 0·60±0·09	
Length of abdominal tergites 9+10	(26) 0·44–0·68, mean 0·53±0·06	
Subgenital plate/abdominal tergites 9+10	(23) 0·73–1·50, mean 1·14±0·20	

DISCUSSION. This species, originally described from Formentera and since found in Majorca and Ibiza, is endemic to the Balearic Islands. With the possible exception of four large females from northern Majorca (discussed below), all the specimens we have seen from these islands seem to belong to *angustulus*, although *pulvinatus* and even *albolineatus* have been recorded from Majorca (Ebner, 1931; Kruseman, *in* Harz, 1975: 929). Both sexes of *angustulus* can be distinguished from *pulvinatus* by the relatively long fore and hind wings, and by the large distance from the stigma to the tip of the fore wing, all these being taken as ratios to the length of the hind femur (Figs 10, 11); the small pronotum and hind femur enable both sexes to be distinguished from *albolineatus*. From *chopardi*, which could also conceivably occur in the Balearic Islands, it can be distinguished by the prominent and narrow pronotal lateral carinae. The fact that *angustulus* males are closely associated with *chopardi* and well-separated from *pulvinatus* on the triangular graph shown in Fig. 13 suggests the possibility that *angustulus* is an island derivative from Iberian stock of *chopardi*.

Not surprisingly, the Formenteran and Ibizan specimens we have examined differ slightly from the Majorcan ones. The Formenteran holotype and allotype show a tendency for the pronotal lateral carinae to be more incurved than is typical of Majorcan specimens, in which these carinae are usually straight in the prozona. The single Ibizan male we have examined (from Talamanca) is unusually small, giving smaller values than any other male for most of the measurements taken; the two Ibizan females examined (from Santa Eulalia del Río) were of more typical size for *angustulus*.

We have examined four female specimens from northern Majorca (one from Puerto de Pollensa, on loan from the Instituut voor Taxonomische Zoölogie, Amsterdam, and three from Alcudia, on loan from the MNHU, Berlin) that are considerably larger than any other Balearic specimens we have seen. The larger size is shown particularly by the following measurements taken from these specimens: length of pronotum 3·6–3·9 mm, length of hind femur 12·1–12·6 mm, length of fore wing 15·5–16·8 mm, length of hind wing 14·3–16·2 mm, distance from stigma to tip of fore wing 0·60–0·71 mm. The hind femora of the largest of these females are as long as those of the smallest female we have examined of *albolineatus*, and there is a small overlap in the length of the pronotum; however, the ratios of both the fore and hind wings to the hind femur in all four specimens give values that are well outside the range of these ratios in our sample of *albolineatus*. It is impossible to form definite conclusions about these four specimens without further material, and in particular associated males, but they could be no more than a large local variant of *angustulus*. It may be significant that the Albufera marsh lies just south of Alcudia; this area of marshland, which is quite unique in the Balearic Islands, could conceivably have been the source of these specimens.

MATERIAL EXAMINED

Holotype (see p. 137) and 42 other specimens from the following localities.

Balearic Islands. Formentera: Can Marti. Ibiza: Talamanca; Santa Eulalia del Río. Majorca: Palma; Palma Nova; Sóller; Puerto de Sóller; Puerto de Pollensa; Capdella.

DISTRIBUTION. Known only from the Balearic Islands.

General discussion

Groups of morphologically very similar species are quite common in the Gomphocerinae. When the members of such a group intermingle in the same habitat, there are usually obvious differences between the calling songs of the males. This is not surprising since it is now generally believed – and has been proved experimentally in some cases – that such song differences provide the main reproductive isolating mechanism. The three main western European species of *Euchorthippus* – *declivus, pulvinatus* and *chopardi* – are sufficiently similar morphologically for misidentification to be frequent. In attempting to assign the 244 males we had at our disposal to one or other of these species on the basis of the shape and length of the subgenital plate (the character on which most emphasis has been placed in the past), we soon found that they showed a continuous gradation from the longest and most pointed *declivus* to the shortest and bluntest *chopardi*, and a large number of males defied identification on this character alone. (In terms of length, the overlap in this character can be seen clearly in Fig. 85.) Since we knew it was not unusual for two of the species to be found together, and there was no *obvious* difference in the male calling songs, we began to wonder whether they were no more than forms of a single species.

The clear morphological separation achieved by the combination of characters used in Fig. 12 made us more confident that three species were involved, and we then turned to the song in the hope of finding some evidence of an ethological barrier. Careful analysis gradually revealed differences that, although subtle and mostly undetectable by the unaided human ear, seemed sufficiently clear to provide a basis for mate recognition. It is perhaps significant that the difference in the male calling song is smallest between *declivus* and *chopardi*, which as far as we know have never been found together; *pulvinatus*, which quite often occurs with either *declivus* or *chopardi*, has a noticeably higher echeme repetition rate than either of them in addition to the further differences revealed by oscillographic analysis.

The close resemblance in both morphology and song shown by these three species suggests that they evolved from a common ancestor quite recently, probably during the Pleistocene Period. The Pleistocene glaciations, during which such an ancestor would no doubt have been pushed southwards into the Iberian, Italian and Balkan Peninsulas, seem likely to have provided the geographical separations that would have tended to lead to morphological and ethological divergence. As can be seen from Fig. 81, there are some anomalies in the distribution of these species that we think can also be explained by the Pleistocene fluctuations in climate. These are the apparent absence of *declivus* from most of the Iberian Peninsula, in spite of its being widespread in Italy and the Balkan Peninsula; the opposite situation in *pulvinatus*, which is common in the Iberian Peninsula but apparently absent from Italy and rare in the Balkans; and the large apparent gap between the western and eastern populations of *pulvinatus*, i.e. between *p. gallicus* and *p. pulvinatus*.

One possibility is that *declivus* evolved from a population of ancestral stock isolated in the Italian Peninsula during a prolonged glacial period. In the course of subsequent warmer climatic phases such a population would have been able to spread northwards, eventually extending its range into much of western and eastern Europe, while leaving in the peninsula the existing Italian populations of *declivus* (which would have had to become adapted to the ameliorating climate). The poor penetration of *declivus* into the Iberian Peninsula could well be explained by the major barrier of the Pyrenees together with competition by other species of *Euchorthippus* already well adapted to the very hot, dry summers of the Spanish Meseta.

A population of *Euchorthippus* isolated in the Iberian Peninsula, perhaps during the same glacial period, could have given rise to *pulvinatus gallicus* as a result of a rather smaller divergence from the main body of the ancestral stock (now *pulvinatus pulvinatus*) occurring in the Balkan Peninsula and further east. Competition with *declivus*, perhaps by then well

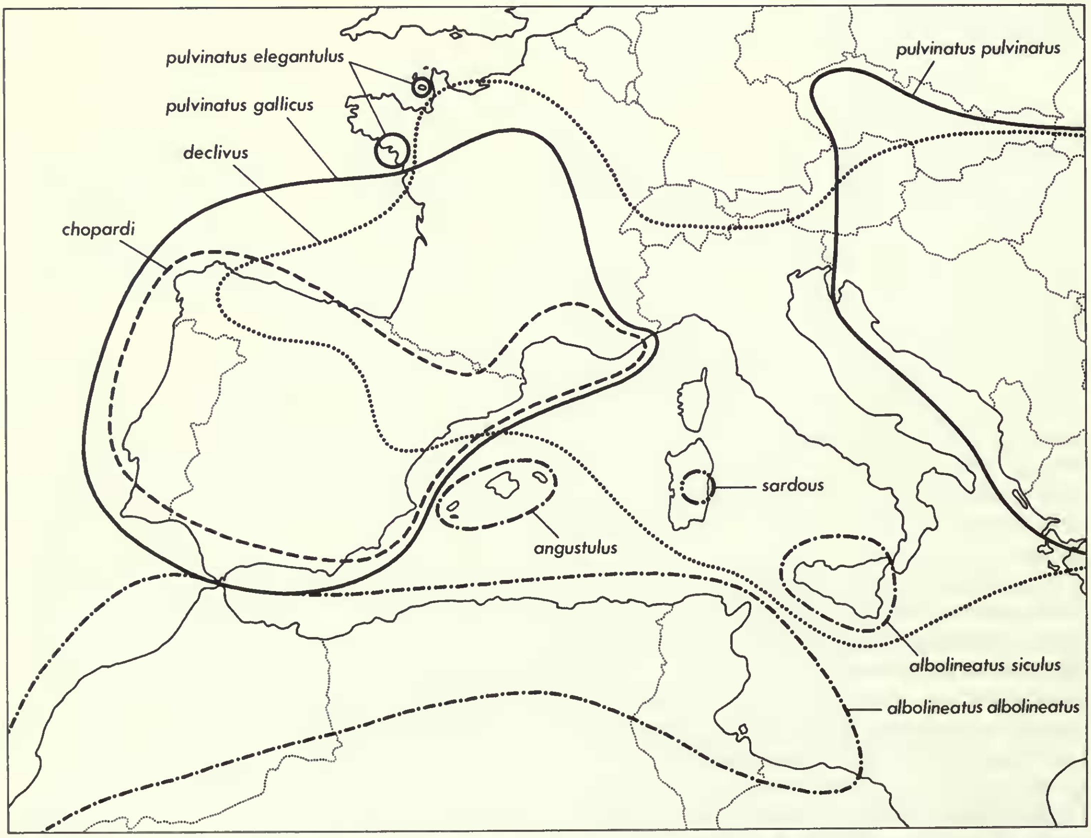


Fig. 81 Map showing the distribution of the western European and North African species of *Euchorthippus*. We regard as doubtful the past records of *E. declivus* from central and southern Spain (see p. 127), *E. pulvinatus* from Italy and Majorca (see pp. 128, 131) and *E. albolineatus* from Portugal, Spain and Majorca (see p. 135), and have therefore not taken them into account in preparing this map.

established in northern Italy and Yugoslavia, could have prevented the western and eastern populations of *pulvinatus* from coming together again.

The evolution of *albolineatus* has no doubt been the result of isolation in North Africa, and we suspect that *chopardi* is a comparatively recent northern derivative from *albolineatus* that has managed to cross the Strait of Gibraltar (perhaps at a time when it was narrower than at present) and thence spread through Spain and past the eastern end of the Pyrenees into southern France, at the same time diverging somewhat from the parental North African stock. Isolation in the Balearic Islands, Sardinia and Sicily, respectively, is sufficient to account for the evolution of *angustulus, sardous* and *albolineatus siculus*. Insular isolation would also account for the morphological divergence of the Jersey population of *p. elegantulus*, though the occurrence of a similar population in southern Brittany suggests that *elegantulus* may be no more than a small northern form of *p. gallicus* occurring in rather unfavourable conditions at the limit of its climatic tolerance.

Although we feel we have been able to throw some further useful light on the taxonomic problems presented by *Euchorthippus*, many questions still remain to be answered. We should welcome the opportunity to record and analyse the song of *albolineatus*, so that its relationship with the European species, particularly *chopardi*, could be better understood. An analysis of the song of the eastern subspecies *p. pulvinatus* would help to establish whether this form is truly conspecific with the western subspecies of *pulvinatus* whose songs are described and analysed in this paper. Information on the songs of *sardous* and *siculus* would also be useful in elucidating their affinities. An experimental test of the effectiveness as an isolating mechanism of the song differences we have detected would be most valuable, as would a further investigation into the related question of hybridization; such studies should take account of the possibility of pheromonal reinforcement of mate recognition, which could conceivably account for the unusually small interspecific song differences in this group. A comparative study of the chromosomes, and particularly the C-banding patterns, of all the western European species might well throw some further light on their inter-relationships. Finally, a comprehensive study of the eastern Palaearctic and Madeiran species of *Euchorthippus*, based on morphology, cytology and song, would lead nearer to a complete understanding of the taxonomy and evolution of this interesting genus.

References

Arana, P., Santos, J. L. & Giraldez, R. 1980. Chiasma interference and centromere co-orientation in a spontaneous translocation heterozygote of *Euchorthippus pulvinatus gallicus* (Acrididae; Orthoptera). *Chromosoma* **78**: 327–340.

Autrum, H. 1963. Anatomy and physiology of sound receptors in invertebrates [pp. 412–433]. *In* Busnel, R.-G. [Ed.], *Acoustic behaviour of animals*. xx+933 pp. Amsterdam.

Azam, J. 1901. Catalogue synonymique et systématique des Orthoptères de France (suite). *Miscellanea Entomologica* **9**: 33–48.

Baccetti, B. 1958. Notulae orthopterologicae. X. Indagini sugli Ortotteri del Gran Sasso d'Italia per il Centro di Entomologia Alpina. *Redia* **43**: 351–450.

Bei-Bienko, G. Ya. 1961. Some features of changes in invertebrate fauna when virgin steppe is cultivated. *Entomologicheskoe Obozrenie* **40**: 763–775. [In Russian. English translation: 1962, *Entomological Review, Washington* **40** (1961): 427–434.]

Bei-Bienko, G. Ya & Mishchenko, L. L. 1951. Locusts and grasshoppers of the U.S.S.R. and adjacent countries. Part II. *Opredeliteli po Faune SSR, Izdavaemye Zoologicheskim Muzeem Akademii Nauk, Leningrad* **40**: 381–667. [In Russian. English translation published by Israel Program for Scientific Translations, Jerusalem, 1964, iv+291+xxi pp.]

Brisout de Barneville, L. 1849. Catalogue des Acridides qui se trouvent aux environs de Paris. *Annales de la Société Entomologique de France* (2) **6** (1848): 411–425.

Broughton, W. B. 1976. Proposal for a new term 'echeme' to replace 'chirp' in animal acoustics. *Physiological Entomology* **1**: 103–106.

Carlson, J. G. 1936. The intergeneric homology of an atypical euchromosome in several closely related Acridinae (order Orthoptera). *Journal of Morphology* **59**: 123–161.

Čejchan, A. 1981. On the orthopteroid insects (s.l.) of Czechoslovakia. I. *Časopis Národního Muzea v Praze* **149** (1980): 125–139. [In Czech with English summary.]

—— 1982. On the orthopteroid insects (s.l.) of Czechoslovakia III. *Časopia Národního Muzea v Praze* **151**: 1–13. [In Czech with English summary.]

Chetyrkina, I. A. 1954. Acridoidea of steppes and deserts of the region of the river Ural. *Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR, Leningrad* **16**: 229–284. [In Russian.]

Chopard, L. 1952. Orthoptéroïdes. *Faune de France* **56** (1951), 359 pp.

Defaut, B. 1982. Quelques précisions sur la détermination, la réparation géographique et l'écologie des espèces françaises du genre *Euchorthippus* [Orth. Acrididae]. *L'Entomologiste* **38**: 82–87.

Descamps, M. 1968. Notes sur le genre *Euchorthippus* [Orth. Acrididae]. Sa répartition dans le Vaucluse et les départements adjacents. *Annales de la Société Entomologique de France* (N.S.) **4**: 5–25.

Ebner, R. 1931. Einige Orthopteren von Mallorca. *Boletín de la Sociedad Española de Historia Natural* **31**: 497–503.

Faber, A. 1953. *Laut- und Gebärdensprache bei Insekten. Orthoptera (Geradflügler).* Teil I. 198 pp. Stuttgart.

Ferrer, E., Lacadena, J. R. & Jódar, B. 1981. Análisis de la asociación somática de cromosomas homólogos en *Euchorthippus pulvinatus gallicus* Maran (Acrididae, Orthopthera [sic]). *Revista de la Real Academia de Ciencias Exactas, Físicas y Naturales de Madrid* **74**: 639–651.

Fischer de Waldheim, G. 1846. Orthoptères de la Russie. *Nouveaux Mémoires de la Société Imperiale des Naturalistes de Moscou* **8**, iv+413 pp.

Galvagni, A. 1956. Primo contributo alla conoscenza degli Ortotteroidei dei Colli Euganei (Veneto). *Memorie del Museo Civico di Storia Naturale di Verona* **5**: 337–359.

Gangwere, S. K. & Morales Agacino, E. 1970. The biogeography of Iberian Orthopteroids. *Miscelánea Zoologica* **2** (5): 1–67.

Géry, J. 1962. Le problème de la sous-espèce et de sa définition statistique (à propos du coefficient de Mayr-Linsley-Usinger). *Vie et Milieu* **13**: 521–541.

González García, M. J. 1981. Contribución al conocimiento de los Acridoidea (Orth.) de la Dehesa Salmantina. *Boletín de la Asociación Española de Entomología* **4** (1980): 55–64.

Harz, K. 1975. Die Orthopteren Europas II. *Series Entomologica* **11**, [viii+] 939 pp.

Herrera Mesa, L. 1979. Contribución al conocimiento de los Acridoideos (Orth. Acridoidea) de la provincia de Navarra. *Boletín de la Asociación Española de Entomología* **3**: 45–64.

—— 1982. Catalogue of the Orthoptera of Spain. *Series Entomologica* **22**, viii+162 pp.

Hewitt, G. M. 1979. Orthoptera. Grasshoppers & crickets. *Animal Cytogenetics* **3** (Insecta 1), v+170 pp.

Jacobs, W. 1953. Verhaltensbiologische Studien an Feldheuschrecken. *Zeitschrift für Tierpsychologie,* Beiheft **1**, vii+228 pp.

Jannone, G. 1937. Contributi alla conoscenza dell'Ortotterofauna italica. 1. Nota preventiva su alcune specie e subspecie nuove opoco note della Puglia e di altre regione dell'Italia meridionale e insulare. *Bolletino di Zoologia, Pubblicato dall'Unione Zoologica Italiana* **8**: 51–76.

John, B. & Hewitt, G. M. 1966. Karyotype stability and DNA variability in the Acrididae. *Chromosoma* **20**: 155–172.

La Greca, M. 1955. Su alcuni Mantodei e Ortotteri italiani poco noti. *Annuario dell'Istituto e Museo di Zoologia dell'Università di Napoli* **6** (1954) (12): 1–11.

—— 1959. L'Ortotterofauna Pugliese ed il suo significato biogeografico. *Memorie di Biogeografia Adriatica, Istituto di Studi Adriatici* **4**: 33–170. [This paper appears to have been issued in separate form well in advance of the relevant part of the journal; we have given the year cited on the separate (1959) in preference to that cited on the journal part (1962).]

Litvinova, N. F. 1972. Patterns of geographic variability of morphological characters in the genus *Euchorthippus* (Orthoptera, Acrididae). *Zoologicheskii Zhurnal* **51**: 821–827. [In Russian with English summary.]

Lucas, H. 1849. Histoire naturelle des animaux articulés. Cinquième classe. Insectes. (Suite.) Deuxième ordre. Les Orthoptères. *Exploration Scientifique de l'Algerie pendant les années 1840, 1841, 1842* (Sciences physiques, Zoologie) **3**: 1–39.

Luquet, G. C. 1978. La systématique des Acridiens Gomphocerinae du Mont Ventoux (Vaucluse) abordée par le biais du comportement acoustique [Orthoptera, Acrididae]. *Annales de la Société Entomologique de France* (N.S.) **14**: 415–450.

Mařan, J. 1954. Die Orthopterenfauna der staatlichen Naturschutzgebiete bei Štúrovo in der Südslowakei (ČSR). *Ochrana Přírody* **9**: 132–139. [In Czech with Russian and German summaries.]

—— 1957. Beitrag zur Kenntnis der europäischen Arten der Gattung *Euchorthippus* Tarb. (Orthoptera, Acrididae). *Acta Entomologica Musei Nationalis Pragae* **31**: 183–190.

Mayr, E. 1969. *Principles of systematic zoology*. xi+428 pp. New York.

McClung, C. E. 1932. Multiple chromosomes in the Orthoptera. *Archivos de la Sociedad de Biología de Montevideo* **7**: 1831–1848.

Nadig, A. & Nadig, A. 1934. Beitrag zur Kenntnis der Orthopteren- und Hymenopterenfauna von Sardinien und Korsika. *Jahresbericht der Naturforschenden Gesellschaft Graubündens* **72**: 3–39.

Pascual, F. 1978. Estudio preliminar de los Ortópteros de Sierra Nevada, I: Introducción general e inventario des especies. *Boletín de la Asociación Española de Entomología* **1** (1977): 163–175.

Perdeck, A. C. 1957. *The isolating value of specific song patterns in two sibling species of grasshoppers (Chorthippus brunneus Thunb. and C. biguttulus L.)*. [viii+] 75 pp. Leiden.

Pitkin, L. M. 1976. A comparative study of the stridulatory files of the British Gomphocerinae (Orthoptera: Acrididae). *Journal of Natural History* **10**: 17–28.

Presa, J. J. 1978. *Los Acridoidea (Orthoptera) de la Sierra del Guadarrama*. 277 pp. Madrid.

Presa, J. J. & García, M. D. 1982. Contribución al conocimiento de los Acridoidea (Orth.) de la región murciana (II): Sierra seca de revolcadores. *Boletín de la Asociación Española de Entomología* **6**: 127–132.

Presa, J. J., Montes, C. & Ramírez-Díaz, L. 1983. Tipificación de poblaciones de saltamontes (Orth. Acrididae) en relación con la altitud, pisos y tipos de vegetación en la Sierra de Guadarrama (Sistema Central, España). *Boletín de la Asociación Española de Entomolgía* **6**: 249–265.

Ramme, W. 1927. Die Dermapteren und Orthopteren Siziliens und Kretas. *Eos* **3**: 111–200.

—— 1931. Beiträge zur Kenntnis der palaearktischen Orthopterenfauna (Tettig. et Acrid.). [I.] *Mitteilungen aus dem Zoologischen Museum in Berlin* **17**: 165–200.

—— 1939. Beiträge zur Kenntnis der palaearktischen Orthopterenfauna (Tettig. u. Acrid.). III. *Mitteilungen aus dem Zoologischen Museum in Berlin* **24**: 41–150.

Santos, J. L. & Giráldez, R. 1982. C-Heterochromatin polymorphism and variation in chiasma localization in *Euchorthippus pulvinatus gallicus* (Acrididae, Orthoptera). *Chromosoma* **85**: 507–518.

Santos, J. L., Arana, P. & Giráldez, R. 1983. Chromosome C-banding patterns in Spanish Acridoidea. *Genetica* **61**: 65–74.

Schmidt, G. H. & Schach, G. 1978. Biotopmässige Verteilung, Vergesellschaftung und Stridulation der Saltatorien in der Umgebung des Neusiedlersees. *Zoologische Beiträge* (N.F.) **24**: 201–308.

Sellier, R. 1947. Matériaux pour un catalogue des Orthoptères et Dermaptères de Bretagne. Première liste. *Bulletin de la Société Scientifique de Bretagne* **21** (1946): 113–122.

Tarbinskii, S. P. 1925. Materials concerning the Orthopterous fauna of the province of Altai. *Russkoe Entomologicheskoe Obozrenie* **19**: 175–195. [In Russian with English summary.]

Tsyplenkov, E. P. 1970. *Harmful Acridoidea of the U.S.S.R.* 272 pp. Leningrad. [In Russian. English translation published by Amerind Publishing Co., New Delhi, 1978, viii+208 pp.]

Uvarov, B. P. 1926. New or less known Acrididae from Central Asia. *Eos* **2**: 321–359.

White, M. J. D. 1972. The value of cytology in taxonomic research on Orthoptera [pp. 27–33]. *In* Hemming, C. F. & Taylor, T. C. H. [Eds], *Proceedings of the International Study Conference on Current and Future Problems of Acridology, London, United Kingdom, 6–16 July 1970*. xv+533 pp. London.

Zeuner, F. E. 1940. The Orthoptera Saltatoria of Jersey, Channel Islands. *Proceedings of the Royal Entomological Society of London* (B) **9**: 105–110.

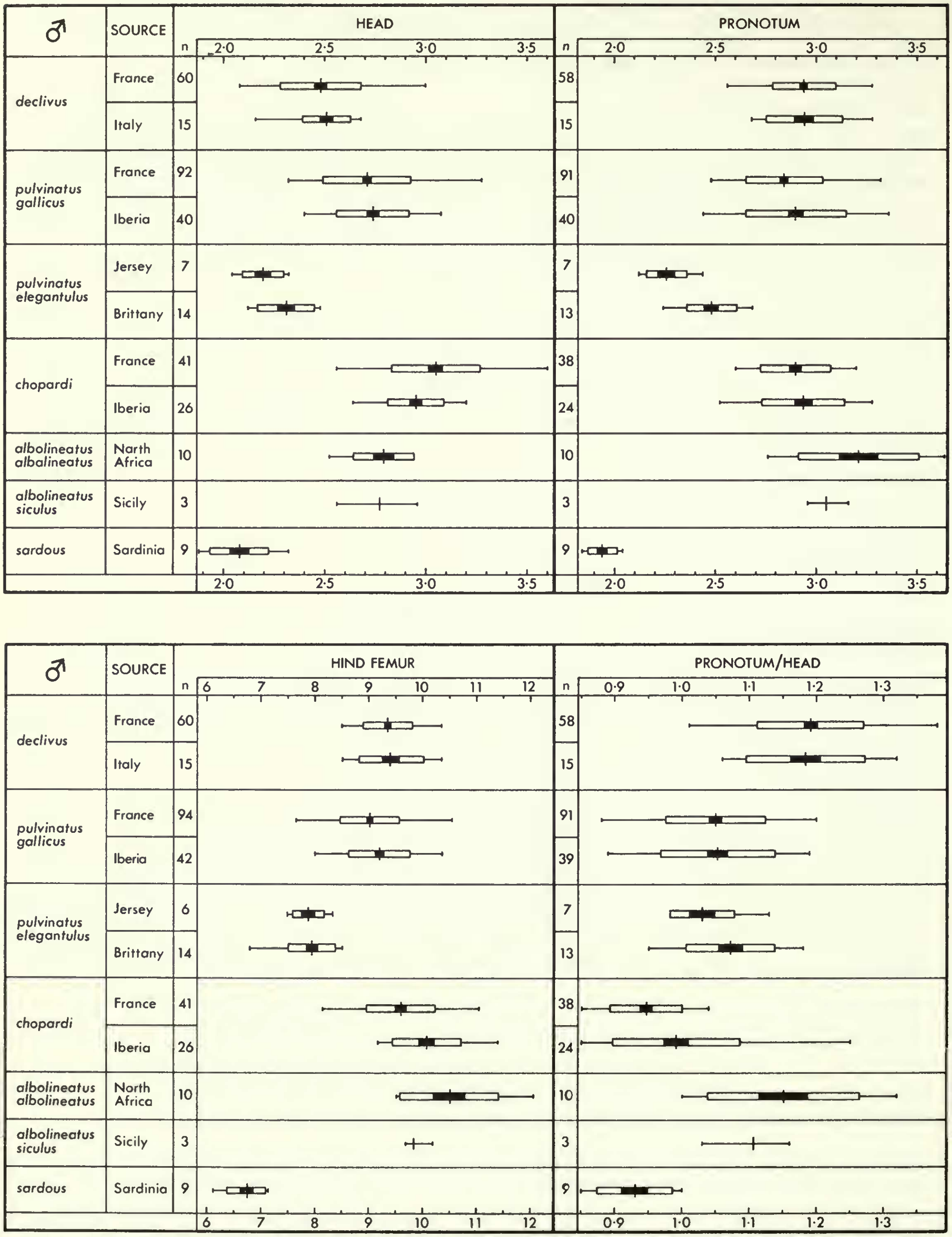


Fig. 82 Data for length of head, length of pronotum, length of hind femur, and length of pronotum divided by length of head, in males of *Euchorthippus*. Measurements are given in millimetres. For explanation of the bars see Fig. 7 (p. 110).

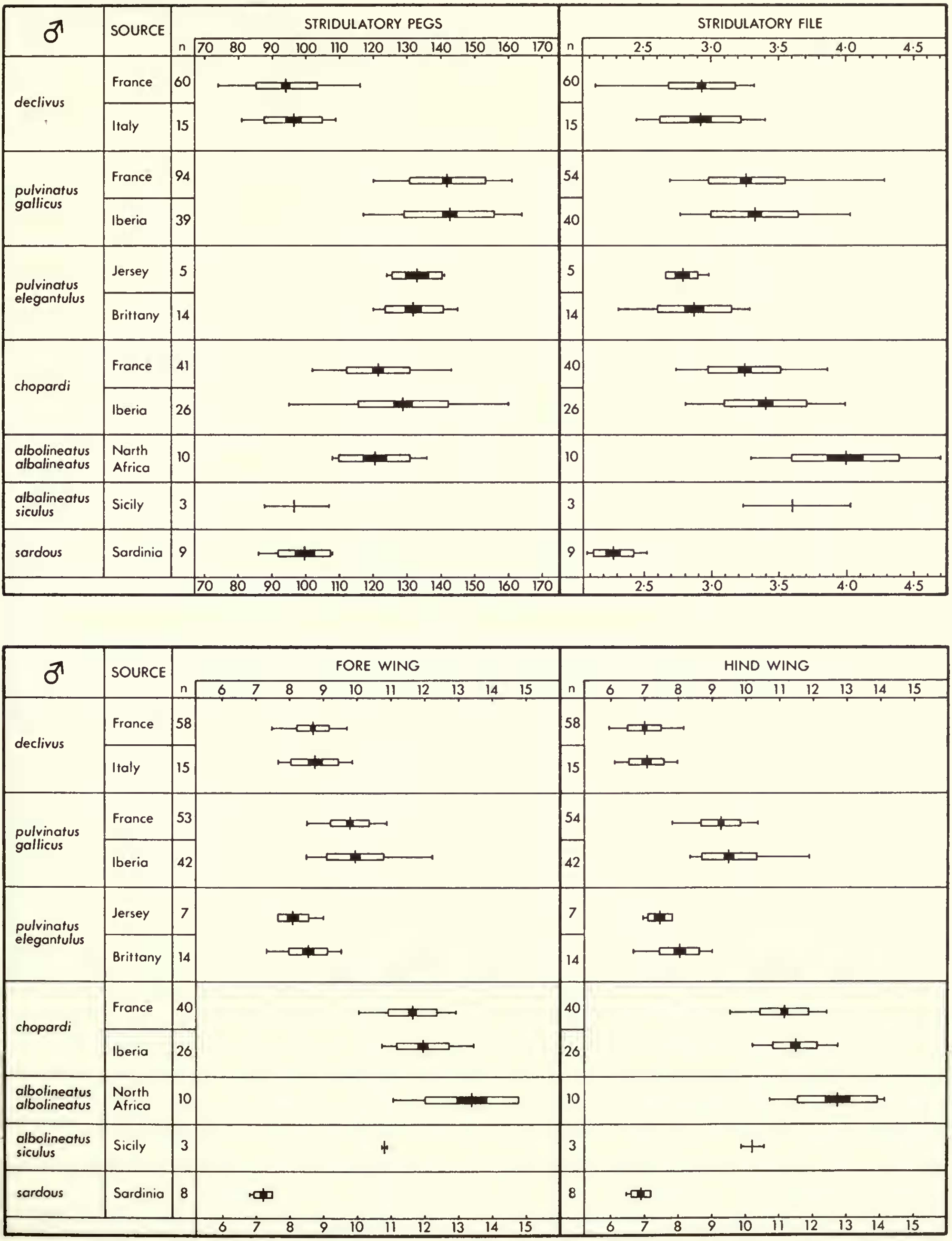


Fig. 83 Data for number of stridulatory pegs, length of stridulatory file, length of fore wing and length of hind wing in males of *Euchorthippus*. Measurements are given in millimetres. For explanation of the bars see Fig. 7 (p. 110).

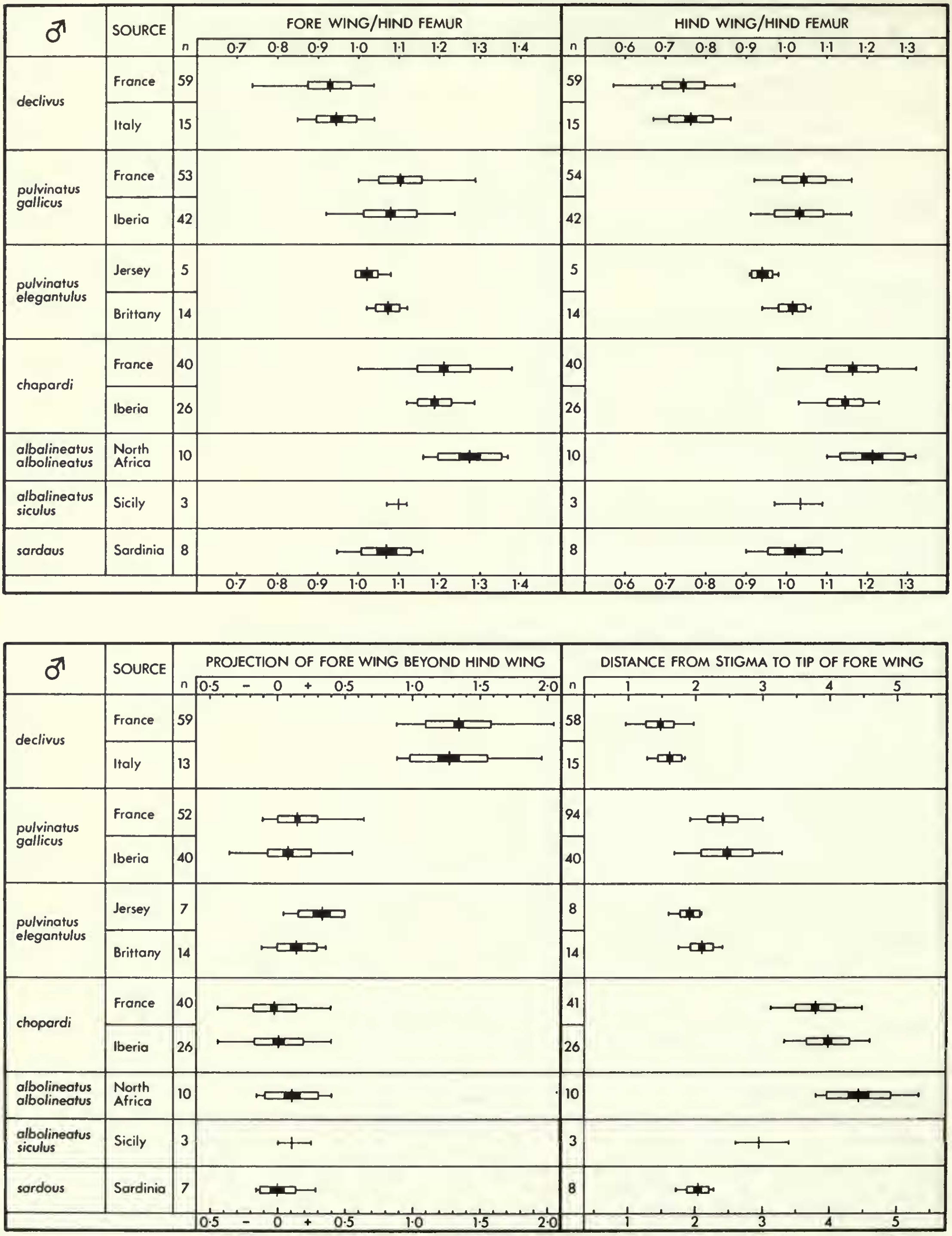


Fig. 84 Data for length of fore wing divided by length of hind femur, length of hind wing divided by length of hind femur, projection of fore wing beyond hind wing, and distance from stigma to tip of fore wing, in males of *Euchorthippus*. Measurements are given in millimetres. For explanation of the bars see Fig. 7 (p. 110).

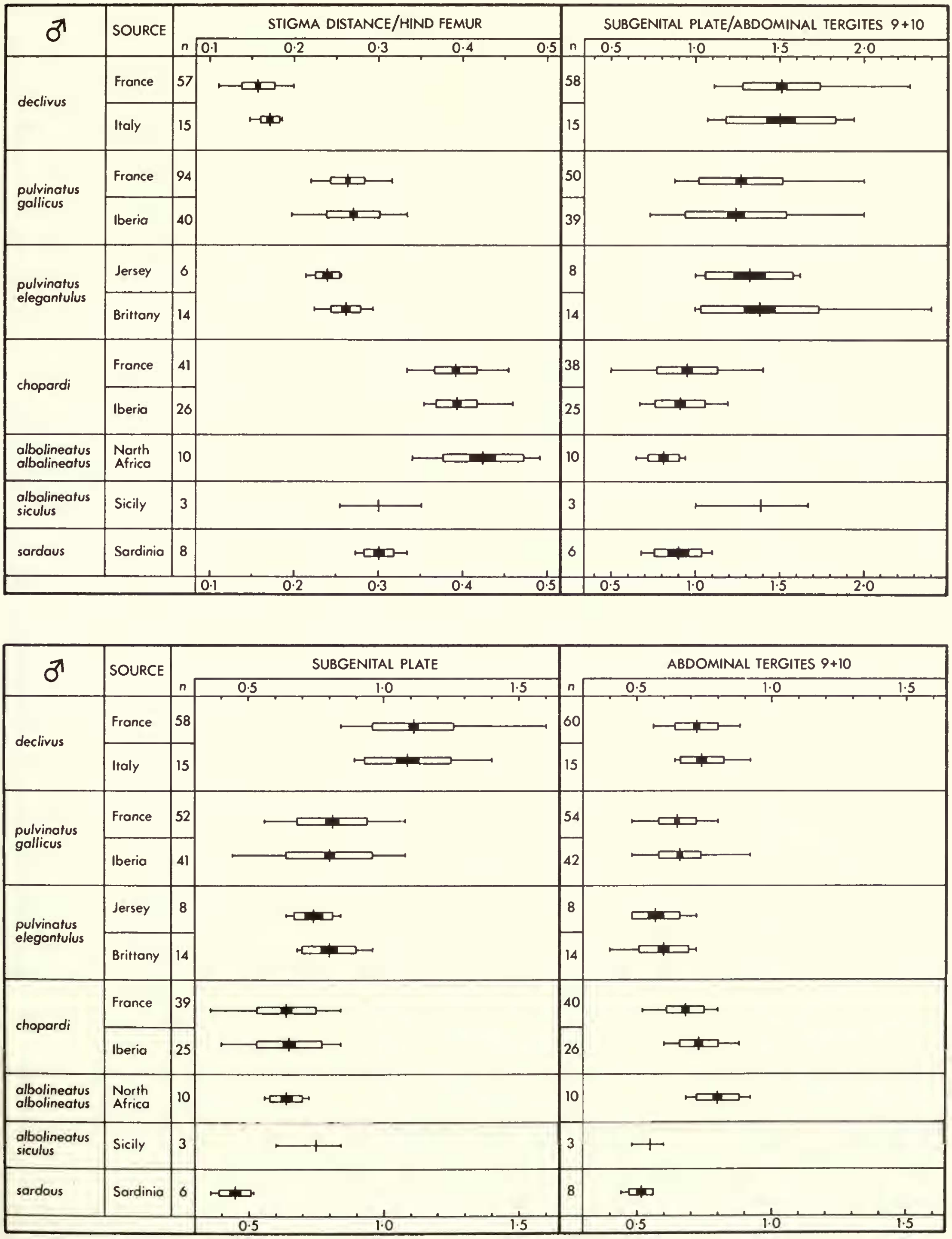


Fig. 85 Data for distance from stigma to tip of fore wing divided by length of hind femur, length of subgenital plate divided by length of abdominal tergites 9+10, length of subgenital plate, and length of abdominal tergites 9+10, in males of *Euchorthippus*. Measurements are given in millimetres. For explanation of the bars see Fig. 7 (p. 110).

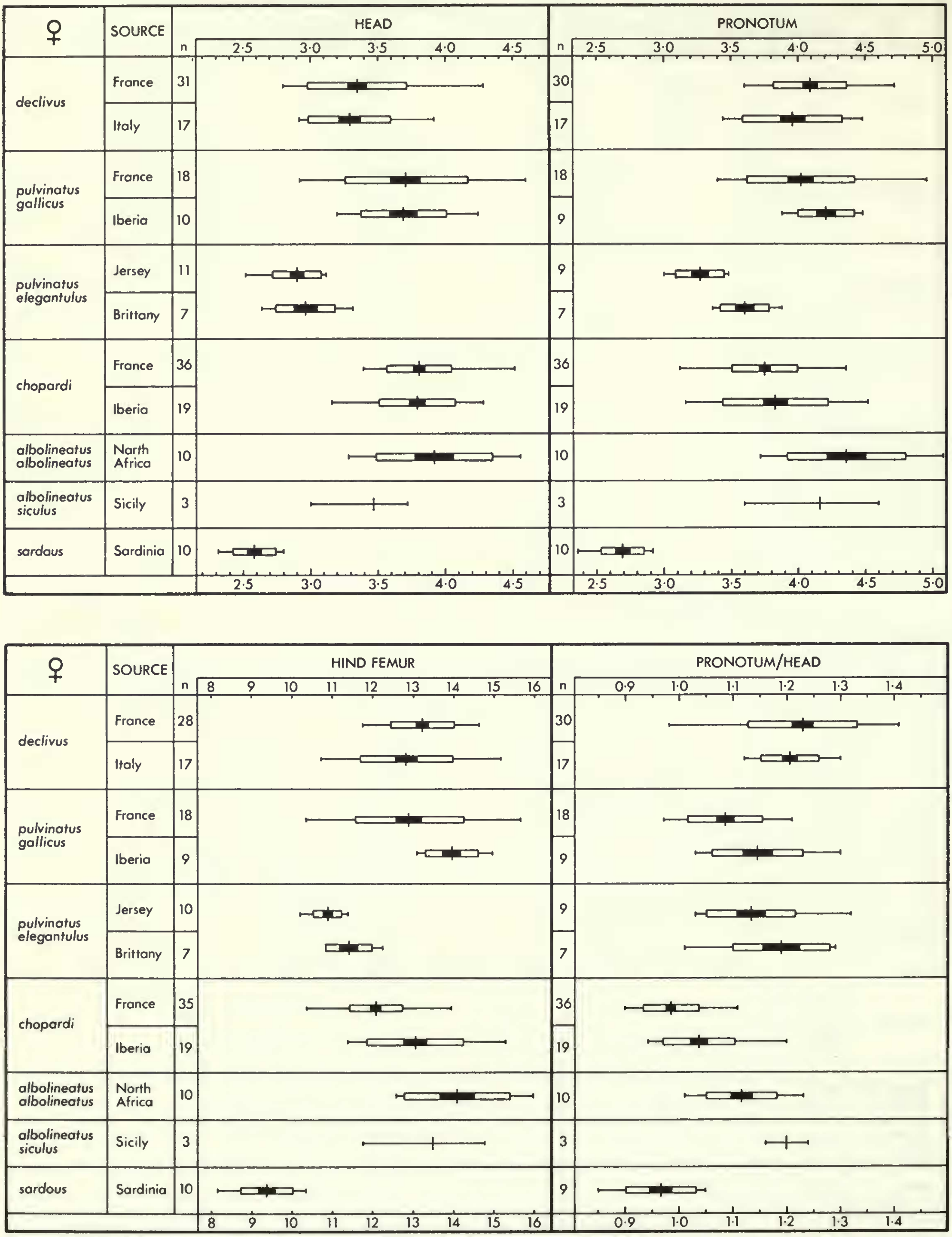


Fig. 86 Data for length of head, length of pronotum, length of hind femur, and length of pronotum divided by length of head, in females of *Euchorthippus*. Measurements are given in millimetres. For explanation of the bars see Fig. 7 (p. 110).

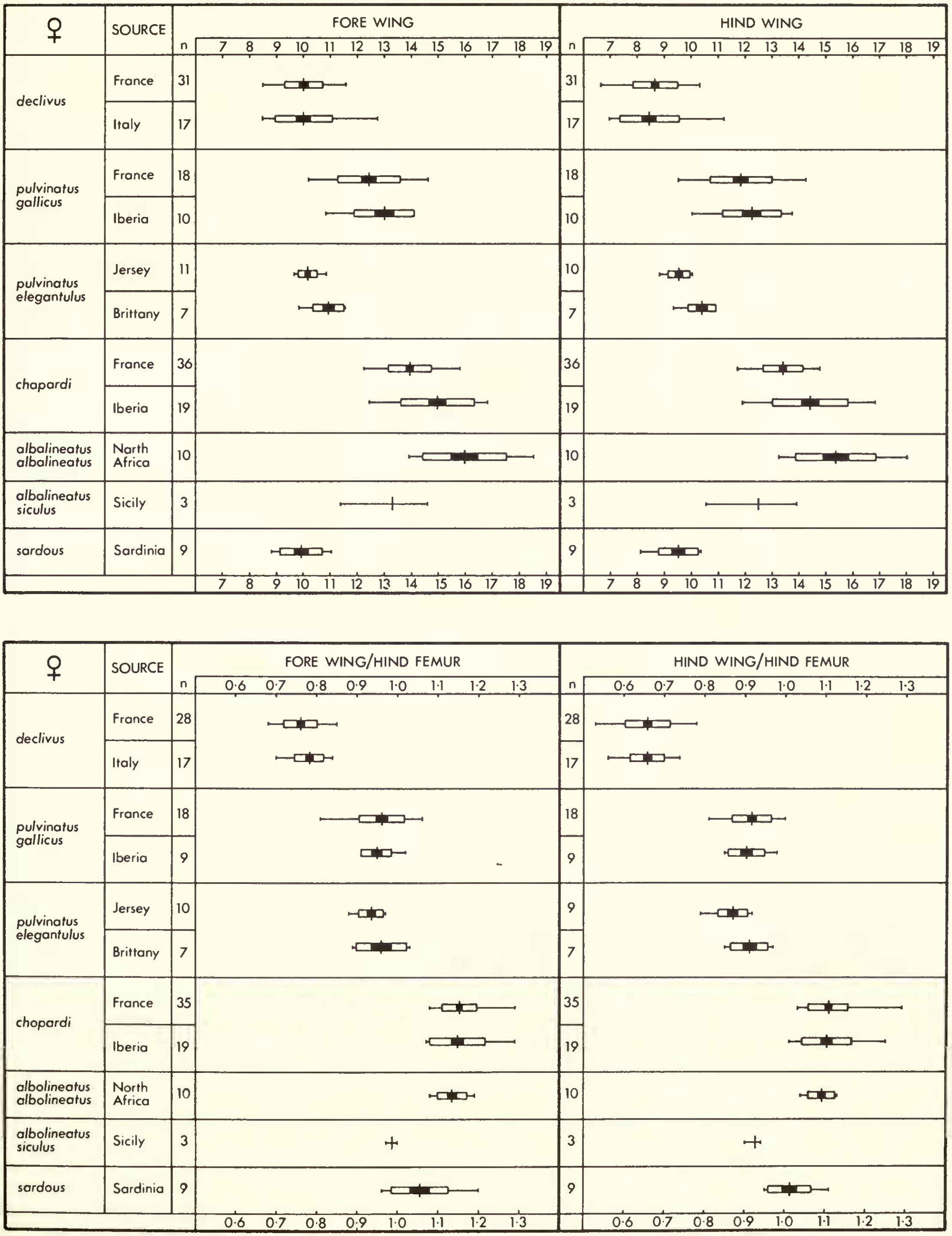


Fig. 87 Data for length of fore wing, length of hind wing, length of fore wing divided by length of hind femur, and length of hind wing divided by length of hind femur, in females of *Euchorthippus*. Measurements are given in millimeters. For explanation of the bars see Fig. 7 (p. 110).

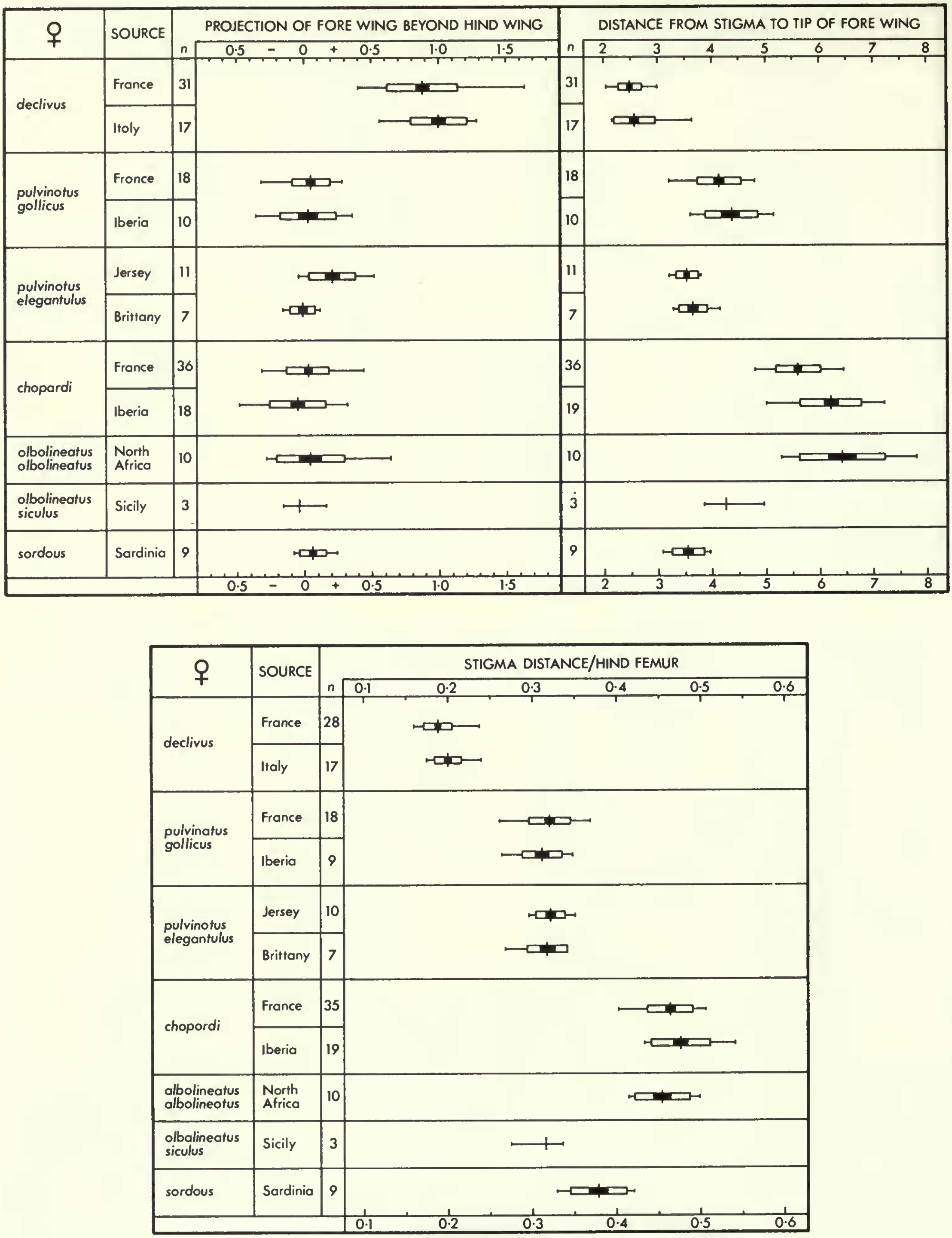


Fig. 88 Data for projection of fore wing beyond hind wing, distance from stigma to tip of fore wing, and distance from stigma to tip of fore wing divided by length of hind femur, in females of *Euchorthippus*. Measurements are given in millimetres. For explanation of bars see Fig. 7 (p. 110).

Index

Invalid names are in *italics*; principal page references in **bold**.

albolineatus 111, 112, 113, 116, 117, 122, 124, 133, **134,** 138, 139, 141
albopunctata 121
alini 121
angustulus 111, 112, 116, 121, 122, 124, **137,** 141
arabicus 122

brachyptera 121

chenbaensis 122
cheui 122
chopardi 110, 111, 112, 113, 114, 115, 116, 117, 119, 120, 121, 122, 126, 127, 128, **133,** 135, 136, 137, 138, 139, 141
Chorthippus 121
Chrysochraon 121

declivus 110, 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 122, **125,** 128, 131, 132, 133, 136, 139, 140
dichrous 121
dispar 121
dorsatus 121

elegantulus 113, 114, 115, 119, 124, 126, 128, **131,** 141

gallicus 112, 113, 114, 115, 116, 117, 119, 124, 127, 128, 129, **131,** 132, 133, 140, 141
gracilis 125, 126

madeirae 122, 126
meridionalis 125, 126
Metrioptera 121
montanus 121

parallelus 121
Platycleis 121
pulvinatus 104, 110, 111, 113, 115, 116, 117, 118, 119, 120, 121, 122, 124, 126, **127,** 135, 136, 137, 138, 139, 140, 141

sabulosa 121
sardous 112, 115, 116, 122, **136,** 141
siculus 112, 115, 116, 134, 135, **136,** 141
Sinhippus 121
štíchai 125

transcaucasicus 122

unicolor 121, 122

weichowensis 122

yungningensis 122